

Cuadro 1. Combinaciones nuevas propuestas por Cabral y Bacigalupo (1997) con sus nombres actuales equivalentes.

Nombres actuales	Combinaciones nuevas
<i>Borreria anthospermoides</i> DC.	<i>Galianthe bogotensis</i> (Kunth) E. L. Cabral & Bacigalupo
<i>Borreria dichasia</i> Sucre & C. G. Costa	<i>Galianthe dichasia</i> (Sucre & C. G. Costa) E. L. Cabral
<i>Diodia brasiliensis</i> Spreng.	<i>Galianthe brasiliensis</i> (Spreng.) E. L. Cabral & Bacigalupo
<i>Diodia brasiliensis</i> var. <i>angulata</i> (Benth.) Standl.	<i>Galianthe brasiliensis</i> subsp. <i>angulata</i> (Benth.) E. L. Cabral & Bacigalupo
<i>Diodia cymosa</i> Cham.	<i>Galianthe cymosa</i> (Cham.) E. L. Cabral & Bacigalupo
<i>Knoxia dichotoma</i> Willd. ex Roem. & Schult.	<i>Galianthe dichotoma</i> (Willd. ex Roem. & Schult.) E. L. Cabral & Bacigalupo
<i>Diodia hispidula</i> A. Rich. ex DC.	<i>Galianthe hispidula</i> (A. Rich. ex DC.) E. L. Cabral & Bacigalupo
—	<i>Galianthe humilis</i> E. L. Cabral & Bacigalupo
—	<i>Galianthe polygonoides</i> E. L. Cabral & Bacigalupo
—	<i>Galianthe vaginata</i> E. L. Cabral & Bacigalupo

especies lo constituye la inclusión de *Diodia brasiliensis* Spreng., *D. cymosa* Cham., *D. hispidula* A. Rich. ex DC., *Knoxia dichotoma* Willd. ex Roem. & Schult., *Diodia brasiliensis* var. *angulata* (Benth.) Standl., en *Galianthe* (Cabral & Bacigalupo, 1997, en este volumen). Al mismo tiempo se incorpora *Borreria anthospermoides* DC.; todas estas especies poseen, como *Galianthe*, frutos dehiscentes, flores heterostilas o dimorfas e inflorescencias casi siempre complejas, tirsoideas o cimoidales, con inflorescencias parciales en dicasios más o menos congestos. Si bien, a diferencia de *Galianthe* que posee frutos con mericarpios dehiscentes, los mericarpios de estas especies son indehiscentes. Por esta razón se las ha agrupado en un nuevo subgénero: *G.* subg. *Ebelia* (Rchb.) E. L. Cabral & Bacigalupo (1997). Dentro de este subgénero están comprendidas además, *Galianthe dichasia* (Sucre & C. G. Costa) E. L. Cabral, *G. humilis* E. L. Cabral & Bacigalupo, *G. polygonoides* E. L. Cabral & Bacigalupo y *G. vaginata* E. L. Cabral & Bacigalupo.

En el Cuadro 1 se da las equivalencias entre los nombres conocidos y las combinaciones nuevas propuestas por Cabral y Bacigalupo, de las especies comprendidas en *Galianthe* subg. *Ebelia*.

ANTECEDENTES

De este grupo de especies son pocas las que han sido estudiadas anteriormente desde el punto de vista palinológico. Galati en su Tesis Doctoral (Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, 1988, inédito), al estudiar la embriología de la tribu Spermacoceae, analiza el polen de 7 géneros y 19 especies, entre ellas *Diodia brasiliensis* y ya señala la coincidencia de caracteres palinológicos y embriológicos entre esta es-

pecie y otras dos, *Borreria fastigiata* (Griseb.) K. Schum. y *B. laxa* Cham. & Schldl., que ahora se consideran dentro de *Galianthe* (Cabral, 1991). Esta coincidencia se refleja también, en la tipología del megagametófito (Galati, 1991).

En un trabajo anterior (Pire & Cabral, 1992), al analizar el valor del polen en la revalidación del género *Galianthe*, se hace referencia a la morfología polínica de *G. dichasia* y de *Borreria anthospermoides*. Esta última especie no fue incorporada dentro de *Galianthe* por Cabral (1991), por presentar frutos con mericarpos indehiscentes y granos de polen con retículo simple, quedando pendiente, en ese momento, su clasificación genérica. A *Borreria dichasia* Sucre & C. G. Costa se la incorporó como *Galianthe dichasia* (Sucre & C. G. Costa) E. L. Cabral, a pesar de sus frutos de mericarpos indehiscentes, porque en ese momento no se disponía de material fructificado y el resto de los caracteres coincidían bien con *Galianthe*.

MATERIAL Y MÉTODOS

Para el estudio de los granos de polen se utilizó anteras de botones florales bien desarrollados, obtenidos de material de herbario. Los ejemplares testigos se encuentran depositados en los siguientes Herbarios: CTES, MBM, MO, NY, SI, SP y RB.

El material palinológico, para su observación con microscopio óptico, fue tratado de acuerdo a la técnica de acetólisis de Erdtman (1966), utilizándose gelatina-glicerina como medio de montaje. Dichos preparados se hallan depositados en la Palinoteca de la Universidad Nacional del Nordeste (PAL-CTES). Para la observación con microscopio electrónico de barrido (MEB) se utilizó polen acetolizado y en algunos casos polen natural, en ambos

casos se los lavó varias veces con agua destilada y se los montó en un trocito de "papel España."

De cada especie se estudió el polen de flores longistilas y brevistilas. Sobre un mínimo de 30 granos, se midieron los parámetros: eje polar y diámetro ecuatorial; en un menor número de granos se midieron: el espesor de la exina, largo y ancho de los colpos, diámetros mayor y menor de las endoaperturas, distancia entre colpos. Además se calculó la relación entre longitud del colpo o ectoapertura (ECA) y longitud del grano o eje polar (P) y se clasificó los colpos en: cortos ($ECA/P = 0.20-0.35$), medianos ($ECA/P = 0.36-0.45$) y largos ($ECA/P = 0.46-0.65$). Estas observaciones se efectuaron utilizando un microscopio óptico Leitz Orthomat. Otras mediciones como, ancho de los muros del retículo, diámetro de los lúmenes, largo y ancho de las espínulas, se realizaron sobre la base de fotomicrografías tomadas con el microscopio electrónico de barrido JEOL-JSMT 100 del Servicio de Microscopía Electrónica de la Facultad de Ciencias Naturales y Museo de la Universidad Nacional de La Plata.

La terminología utilizada es básicamente la de Erdtman (1966) y se consultó también Kremp (1968).

A continuación se cita el material examinado bajo el nombre de la nueva combinación propuesta por Cabral y Bacigalupo y entre barras el basónimo correspondiente.

MATERIAL EXAMINADO

Galianthe bogotensis (Kunth) E. L. Cabral & Bacigalupo [*Borreria anthospermoides* DC.]. Flores brevistilas: COLOMBIA. **Boyacá:** Socha, Fosberg 22225 (NY) [PAL-CTES 3792]. NUEVA GRANADA. J. J. Triana 75 (NY) [PAL-CTES 3952]. Flores longistilas: COLOMBIA. **Boyacá:** Cord. Oriental, Páramo de Belén, H. Barclay & P. Juajibioy 7661 (MO) [PAL-CTES 3120]. **Cundinamarca:** Cordillera Oriental, Páramo, H. García Barriga 16136 (NY) [PAL-CTES 3790].

Galianthe brasiliensis (Spreng.) E. L. Cabral & Bacigalupo [*Diodia brasiliensis* Spreng.]. Flores brevistilas: PARAGUAY. Encarnación, Mboy-caé, Bertoni 2401 (CTES) [PAL-CTES 3175]. Flores longistilas: ARGENTINA. **Misiones:** Candelaria, Cerro Corá, Bertoni 2604 (CTES) [PAL-CTES 3174].

Galianthe brasiliensis subsp. *angulata* (Benth.) E. L. Cabral & Bacigalupo [*Triodon angulatum* Benth.]. Flores brevistilas: MEXICO. **Veracruz:** Jicó, Pringle 10803 (CTES) [PAL-CTES 3404]. Flores longistilas: MEXICO. **Hidalgo:** El Candeje, Gimete 852 (CTES) [PAL-CTES 3789].

Galianthe cymosa (Cham.) E. L. Cabral & Bacigalupo [*Diodia cymosa* Cham.]. Flores brevistilas: BRASIL. **Paraná:** Curitiba, Barigui, Ferreira 186 (MO) [PAL-CTES 3794].

Galianthe dichasia (Sucre & C. G. Costa) E. L. Cabral [*Borreria dichasia* Sucre & C. G. Costa]. Flores brevis-

tilas: BRASIL. **Paraná:** Curitiba, Tessmann 67 (MBM) [PAL-CTES 3077]. Flores longistilas: BRASIL. **Paraná:** Rincão, Hatschbach 624 (SP) [PAL-CTES 3076].

Galianthe dichotoma (Willd. ex Roem. & Schult.) E. L. Cabral & Bacigalupo [*Knoxia dichotoma* Willd. ex Roem. & Schult.]. Flores brevistilas: ECUADOR. **Azuay-Loja:** Nudo de Cordillera Occidental y Cord. Oriental, entre Oña y Rancho Ovejero, Barclay et al. 8454 (MO) [PAL-CTES 3114]. Flores longistilas: ECUADOR. **Pichincha:** Cantón Quito, C. Cerón 2253 (MO) [PAL-CTES 3953]. PERU. **Cajamarca:** camino a laguna Chamis, Sánchez Vega 759 (SI) [PAL-CTES 3407].

Galianthe hispidula (A. Rich. ex DC.) E. L. Cabral & Bacigalupo [*Diodia hispidula* A. Rich. ex DC.]. Flores brevistilas: ARGENTINA. **Misiones:** L. N. Alem, Cabral et al. 496 (CTES) [PAL-CTES 3393]. Flores longistilas: ARGENTINA. **Corrientes:** Santo Tomé, Ea. Timbó, Tressens et al. 1598 (CTES) [PAL-CTES 3787]. **Misiones:** San Ignacio, Schwarz 1699 (CTES) [PAL-CTES 3954].

Galianthe humilis E. L. Cabral & Bacigalupo. Flores longistilas: BRASIL. **Minas Gerais:** Pouso Alegre, Hoehne 19357 (SP) [PAL-CTES 3392].

Galianthe polygonoides E. L. Cabral & Bacigalupo. Flores brevistilas: BRASIL. **Rio de Janeiro:** Petrópolis, Caeteté, D. C. Goés et al. 240 (RB) [PAL-CTES 3788]; Carangola, Goés et al. 500 (RB) [PAL-CTES 3955]. Flores longistilas: BRASIL. **Rio de Janeiro:** Petrópolis, Sucre 4190 et al. (RB) [PAL-CTES 3391].

DESCRIPCIÓN GENERAL DE LOS GRANOS DE POLEN

Las especies de *Galianthe* subg. *Ebelia* constituyen un grupo bastante homogéneo desde el punto de vista palinológico. Los granos de polen presentan las siguientes características: isopolares, radiosimétricos, tamaño mediano (25–50 μm), oblato-esferoidales o prolato-esferoidales. De acuerdo a las aperturas son zono-colporados: 6–7 colporados en *Galianthe brasiliensis* y *Galianthe dichasia* (flores brevistilas) y 8–9(–10) colporados en el resto de las especies. Los colpos generalmente son largos y las endoaperturas lalongadas. La exina, de 2.5–3.5 μm de espesor, es semitectada-reticulada, con retículo complejo diferenciado en un suprarretículo (SR), psilado, y un infrarretículo (IR), espinulado, a un nivel más bajo que el anterior. Se exceptúan *G. bogotensis* y *G. dichotoma* que presentan retículo simple, de muros espinulados.

El SR puede presentar mallas cerradas o abiertas (con muros interrumpidos), que, generalmente, aumentan de tamaño hacia los polos.

El IR se puede encontrar distintamente diferenciado; por lo general, se lo observa como puentes, simples o ramificados, que atraviezan los lúmenes del SR (1), o a veces, reducido a espínulas ubicadas lateralmente en la base de los muros del SR (*G. brasiliensis* y *G. humilis*) (2), o bien, está totalmente ausente y en este caso las espínulas se localizan sobre el SR (*G. dichotoma* y *G. bogotensis*) (3). De este modo, se podrían reconocer 3 estadios

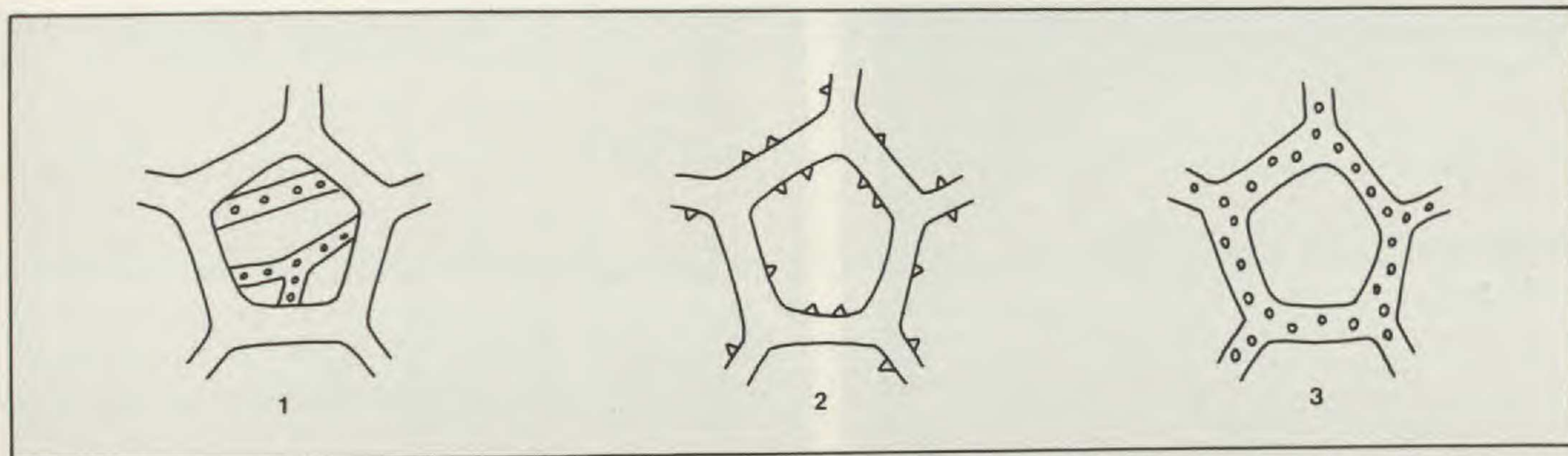


Figura 1. Representación gráfica de los estadios de modificación de la exina entre retículo complejo (1-2) y retículo simple (3).

de modificación de la estructura de la exina, entre retículo complejo y retículo simple (Fig. 1), cuya secuencia evolutiva no puede ser establecida aún con certeza.

Por otra parte, las flores longistilas y brevistilas presentan un dimorfismo polínico poco marcado que está dado por finas diferencias en la ornamentación de la exina y por un tamaño levemente mayor de los granos de polen en flores brevistilas.

DIFERENCIAS ENTRE LAS ESPECIES

Las principales diferencias entre las especies están dadas por:

(1) ORNAMENTACIÓN DE LA EXINA

De acuerdo a ella se pueden agrupar las especies en: con retículo simple o con retículo complejo.

Con retículo simple hay 2 especies: *G. bogotensis* y *G. dichotoma*, que presentan diferencias entre sí. En la primera el retículo posee lúmenes profundos y amplios (de hasta 4.5 μm de ancho), entre los que se intercalan otros menores (0.2 μm) y muros rectilíneos o suavemente curvilíneos, provistos de 1 sola hilera de espínulas (Fig. 2A, C). En la segunda especie, los lúmenes son comprimidos, de contorno muy irregular y de menor tamaño (de 2-3 μm , a veces 3.5 μm de largo \times 0.6-1 μm de ancho), los muros son curvilíneos con 1 ó 2 hileras de espínulas (Fig. 2B, D).

Con respecto al retículo complejo, las variantes observadas corresponden a los 3 tipos básicos ya descritos para otras especies de *Galianthe* (Pire & Cabral, 1992):

TIPO I: SR completo en todo el grano; IR poco visible;

TIPO II: SR interrumpido formando mallas abiertas en los mesocolpos; IR parcialmente visible;

TIPO III: SR reducido a fragmentos pequeños en

la zona ecuatorial; IR parcial a completamente visible.

El TIPO I es el más frecuente, el TIPO II se presenta en *G. brasiliensis* subsp. *angulata* y en *G. cymosa* (Fig. 3A-D) y el TIPO III, sólo en flores brevistilas de *G. polygonoides* (Fig. 3E-G). En el TIPO I los muros del SR son \pm rectilíneos y los lúmenes poligonales, isodiamétricos o alargados. En los TIPOS II y III, los muros son curvilíneos y los lúmenes tienen forma irregular. Con respecto al IR en algunas especies se observaron variaciones en la distribución de las espínulas: en *G. brasiliensis* subsp. *angulata* (flor brevistila) los muros son pobremente espinulados; en mesocolpos poseen 1 ó 2 espínulas y hacia los polos tienden a ser psilados (Fig. 3C); en *G. brasiliensis*, y flores longistilas de *G. humilis*, y *G. polygonoides*, las espínulas se localizan, ya sea sobre los muros que atraviezan los lúmenes de SR o ya sea lateralmente en la base del SR (Figs. 2G, 3E-G, 4).

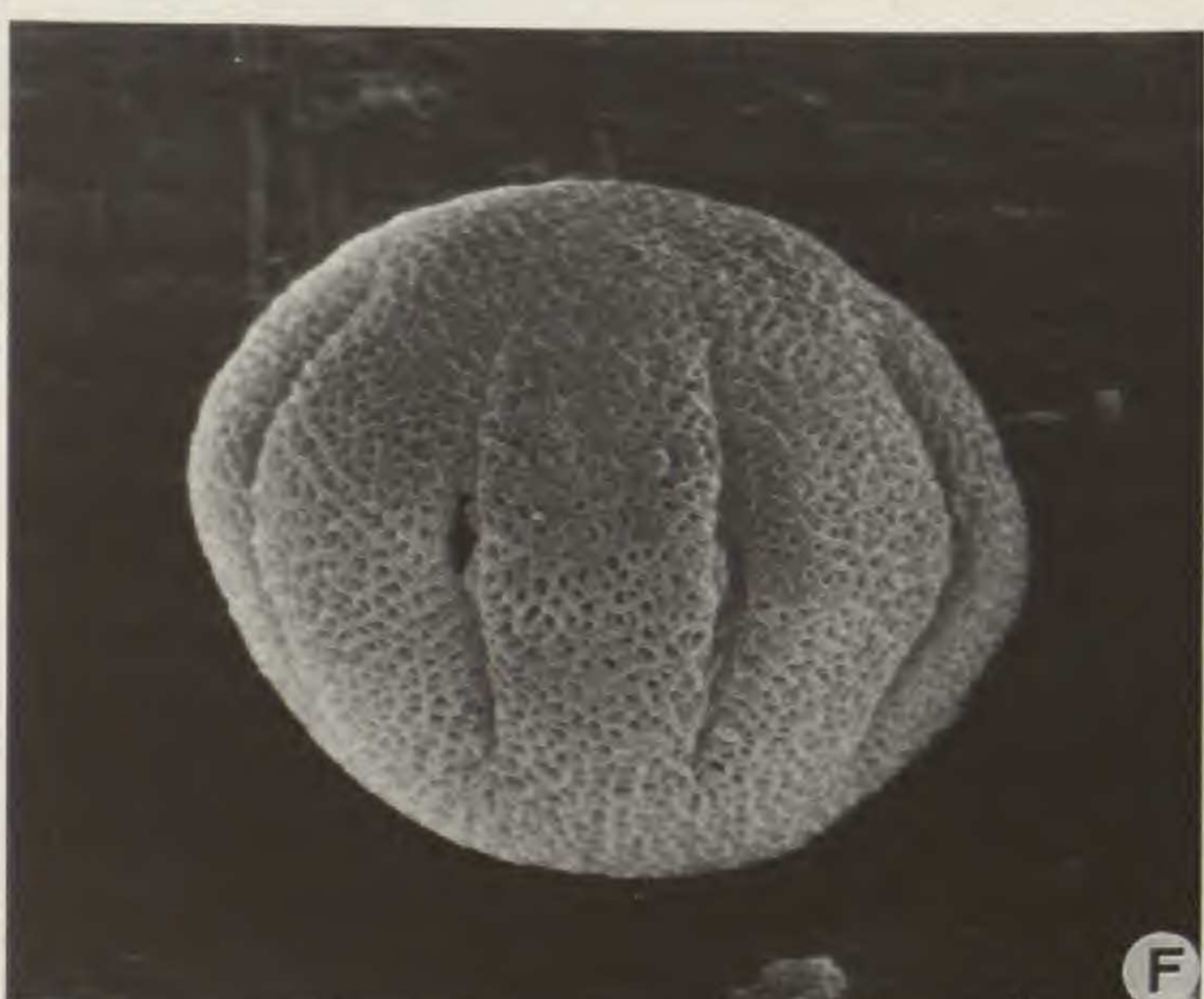
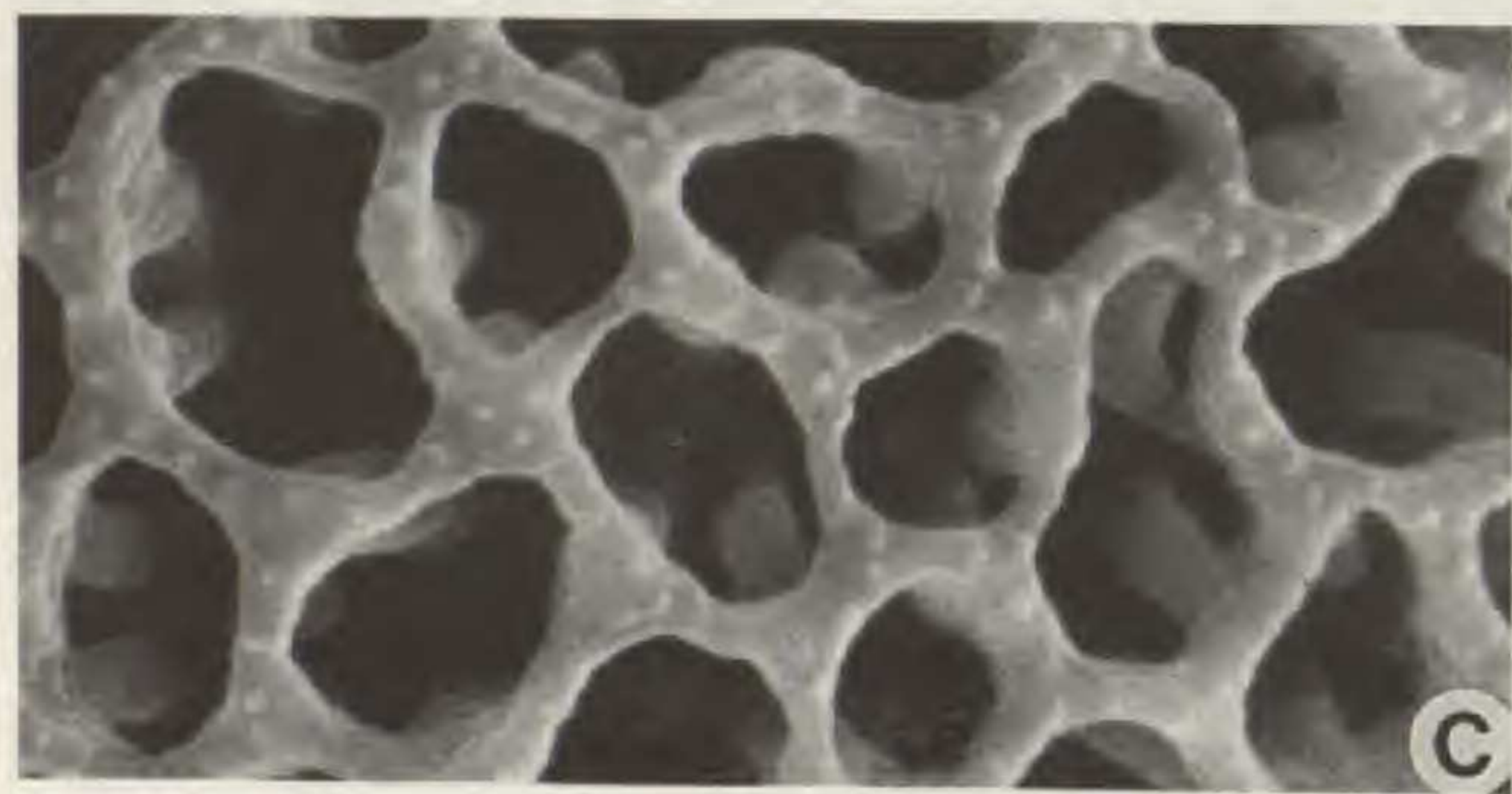
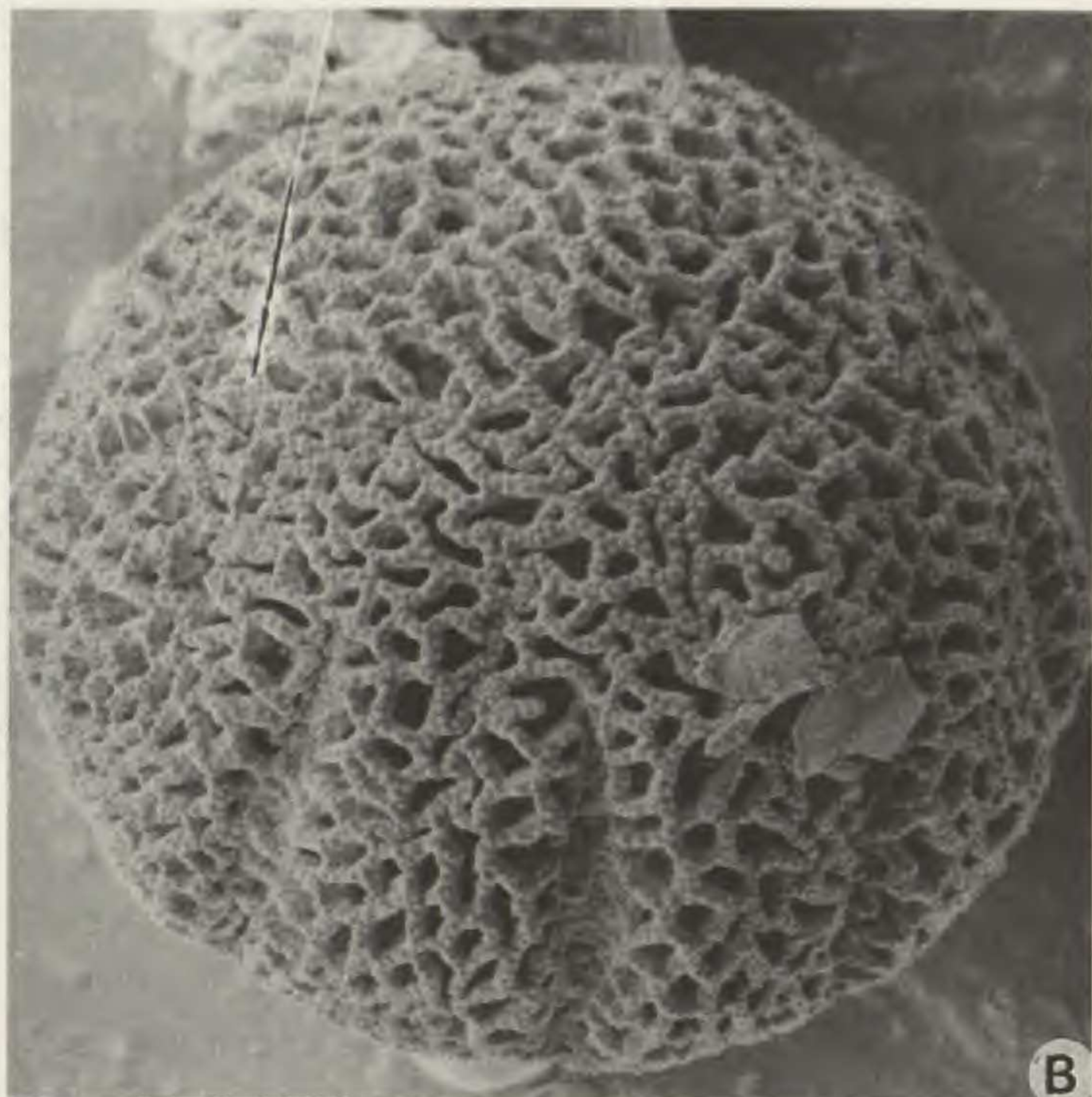
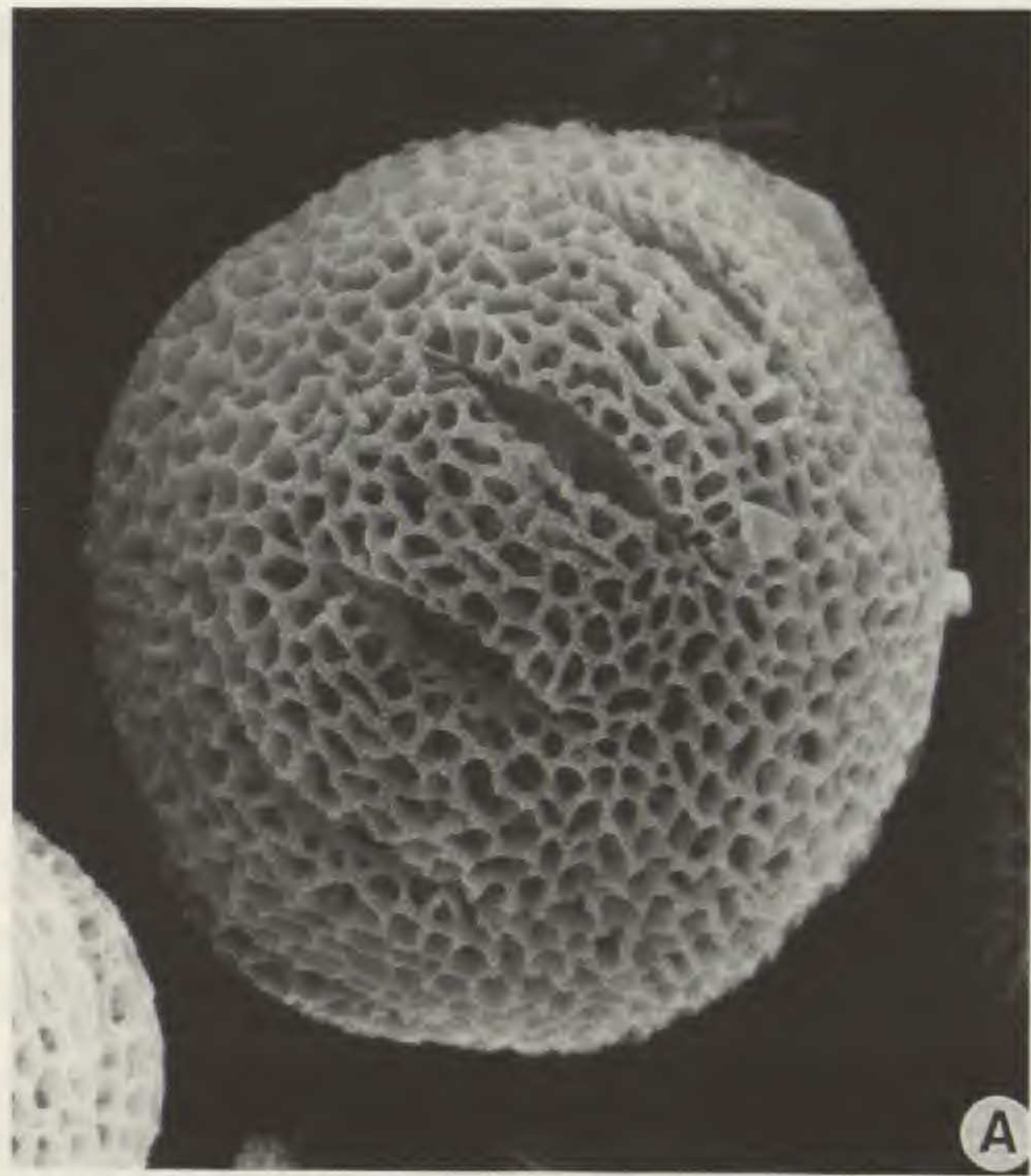
(2) LONGITUD DEL COLPO O ECTOAPERTURA

En todas las especies, excepto *G. bogotensis*, los granos de polen poseen colpos largos (ECA/P mayor de 0.45). Sin embargo, algunas especies, como *G. dichotoma* y las flores longistilas de *G. brasiliensis* subsp. *angulata* y *G. dichasia*, pueden tener, además, granos con colpos medianos (ECA/P = 0.40-0.51). En *G. bogotensis* los colpos pueden ser cortos o medianos (ECA/P = 0.33-0.43).

Otras diferencias respecto al número de aperturas, forma y tamaño de los granos, diámetro de los lúmenes del SR y ancho de los muros del SR e IR, se exponen en el Cuadro 2.

DISCUSIÓN Y CONCLUSIONES

En el Figura 5 se resumen, en forma esquemática, los caracteres exomorfológicos y caracteres palinológicos de los géneros *Galianthe* (subg. *Ebe-*



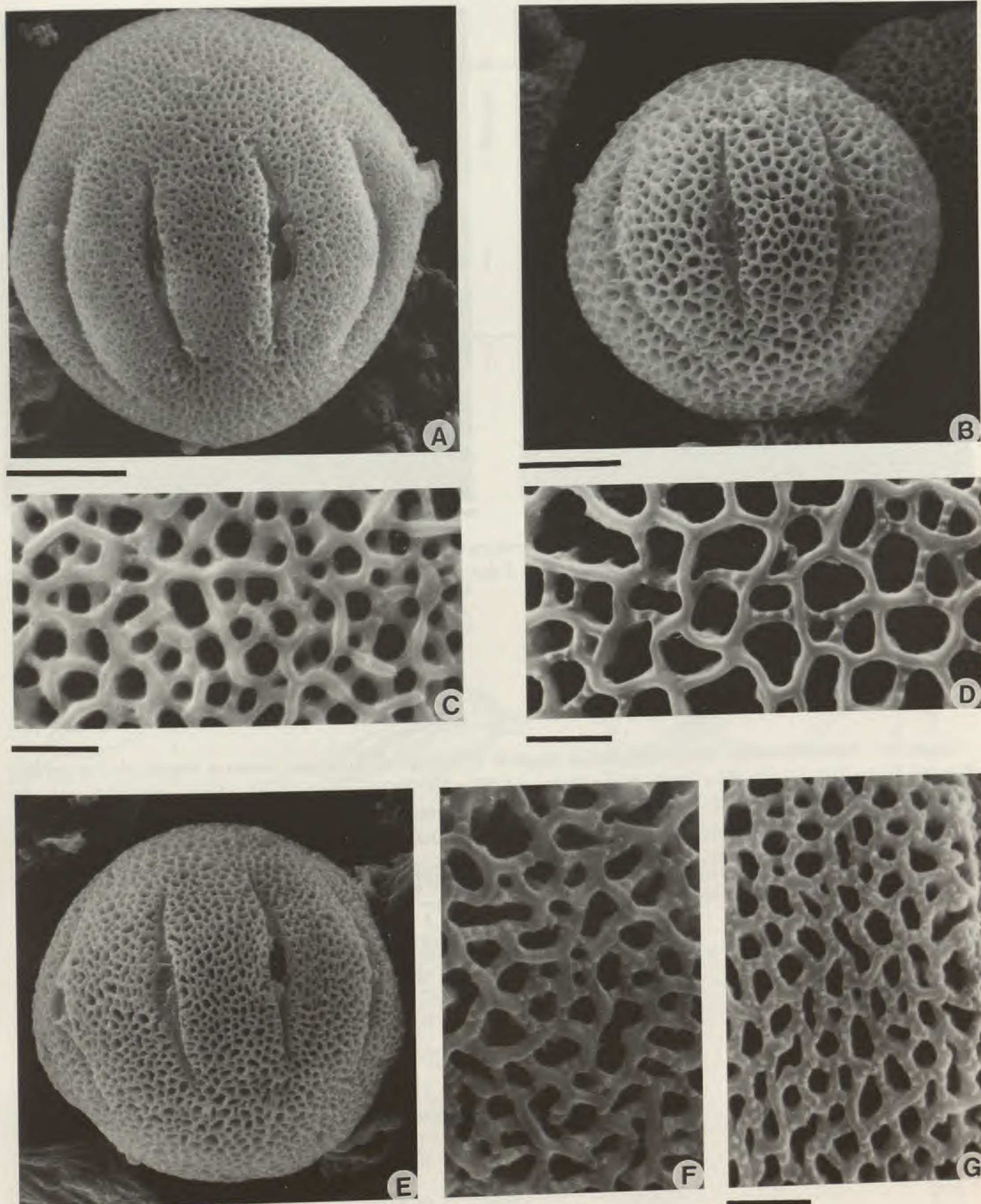


Figura 3. Granos en vista ecuatorial y detalle de la escultura del apocolpio. —A, C. *Galianthe brasiliensis* subsp. *angulata*, f.b. (Pringle 10803). —B, D. *G. cymosa*, f.b. (Ferreira 186). E–G. *G. polygonoides*, f.b. —F. Apocolpio. —G. Mesocolpio (Goés et al. 240). Las escalas equivalen a 10 µm en A, B, E y 2 µm en C, D, F, G. (f.b., flor brevistila; f.l., flor longistila.)

←

Figura 2. Granos en vista ecuatorial y detalle de la escultura del apocolpio. —A, C. *Galianthe bogotensis*, f.b. (Fosberg 22225). —B, D. *G. dichotoma*, f.l. (Sanchez Vega 759). E, G. *G. brasiliensis*. —E. f.b. (Bertoni 2401). —G. f.l. (Bertoni 2604). —F, H. *G. hispidula*, f.l. (Tressens et al. 1598). Las escalas equivalen a 10 µm en A, B, E, F y a 2 µm en C, D, G, H. (f.b., flor brevistila; f.l., flor longistila.)

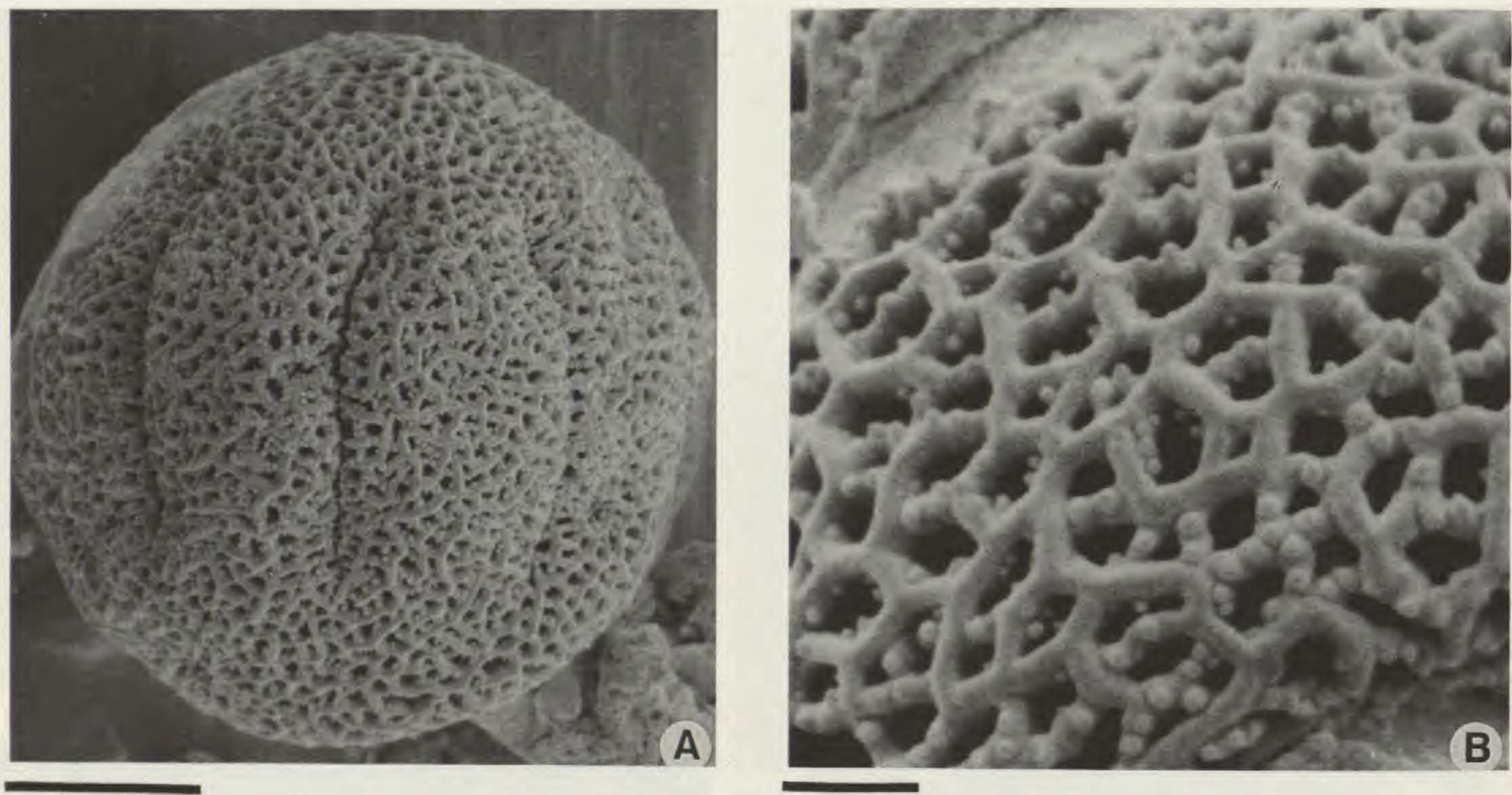


Figura 4. Grano en vista ecuatorial y detalle de la escultura en mesocolpio. —A, B. *Galianthe humilis*, flor longistila (Hoehne 19357). Las escalas equivalen a 10 μ m en A y 2 μ m en B.

Cuadro 2. *Galianthe* subg. *Ebelia*: diferencias respecto al número de aperturas, forma y tamaño de los granos, diámetro de los lúmenes del SR y ancho de los muros del SR y IR. Referencias: obl-esf., oblato-esferoidal; prol-esf., prolato-esferoidal; P, eje polar; E, diámetro ecuatorial; SR, suprarretículo; IR, infrarretículo. Las medidas estan en μ m. Respecto al tamaño de los granos se indica las medidas promedio y de los lúmenes del SR, el diámetro mayor.

Especies	Aperturas	Forma	Tamaño P \times E	SR muros//lúmenes	IR muros
<i>G. bogotensis</i>					
fl. long.	8–9	obl-esf.	38.6 \times 40.8	0.4–0.5//1(2.6)4.5	—
fl. brev.	(7)8–9	obl-esf.	43.0 \times 46.5	0.6–0.9//1.4(3.4)4.5	—
<i>G. brasiliensis</i>					
fl. long.	6(7)	prol-esf.	25.7 \times 24	0.3–0.4//0.3(1.5)2.9	0.15–0.4
fl. brev.	(6)7	obl-esf./prol-esf.	27.3 \times 27.2	0.4–0.7//0.7(2.0)3.3	0.35–0.6
<i>G. brasiliensis</i> subsp. <i>angulata</i>					
fl. long.	(8)10	obl-esf.	27.3 \times 31.5	—	—
fl. brev.	8–9	prol-esf.	36.8 \times 36	0.3–0.6//0.2(1.3)2.8	0.3–0.4
<i>G. cymosa</i>					
fl. brev.	8(9)	prol-esf.	37.6 \times 36.7	0.3–0.4//1.4(2.8)5.8	0.3–0.35
<i>G. dichasia</i>					
fl. long	8	subprol.	42.7 \times 36.2	0.4–0.5//0.5(1.5)2.0	0.35
fl. brev.	7(8–0)	subprol.	41.5 \times 35.3	0.5–0.6//1.0(1.5).18	0.3–0.5
<i>G. dichotoma</i>					
fl. long.	9(10)	obl-esf./prol-esf.	34.0 \times 34.2	0.5–0.7//0.8(2.5)3.5	—
fl. brev.	9	obl-esf.	41.5 \times 35.3	0.5–0.6//1.0(1.5)1.8	0.3–0.5
<i>G. hispidula</i>					
fl. long.	(7)8	obl-esf.	33.0 \times 34	0.3–0.4//0.4(1.2)2	0.2
fl. brev.	(8)9	obl-esf./prol-esf.	34.7 \times 34	0.4–0.5//1(1.2)3	0.3–0.4
<i>G. humilis</i>					
fl. long.	8	prol-esf.	37.3 \times 36.5	0.4–0.5//1(2.1)3.7	0.3–0.4
<i>G. polygonoides</i>					
fl. long.	(7)8	prol-esf.	28.0 \times 26.3	0.3–0.5//0.4(1.4)2.2	0.2–0.35
fl. brev.	(7)8–9	obl-esf.	34.9 \times 36.0	0.35//0.9(1.4)3.8	0.35–0.4

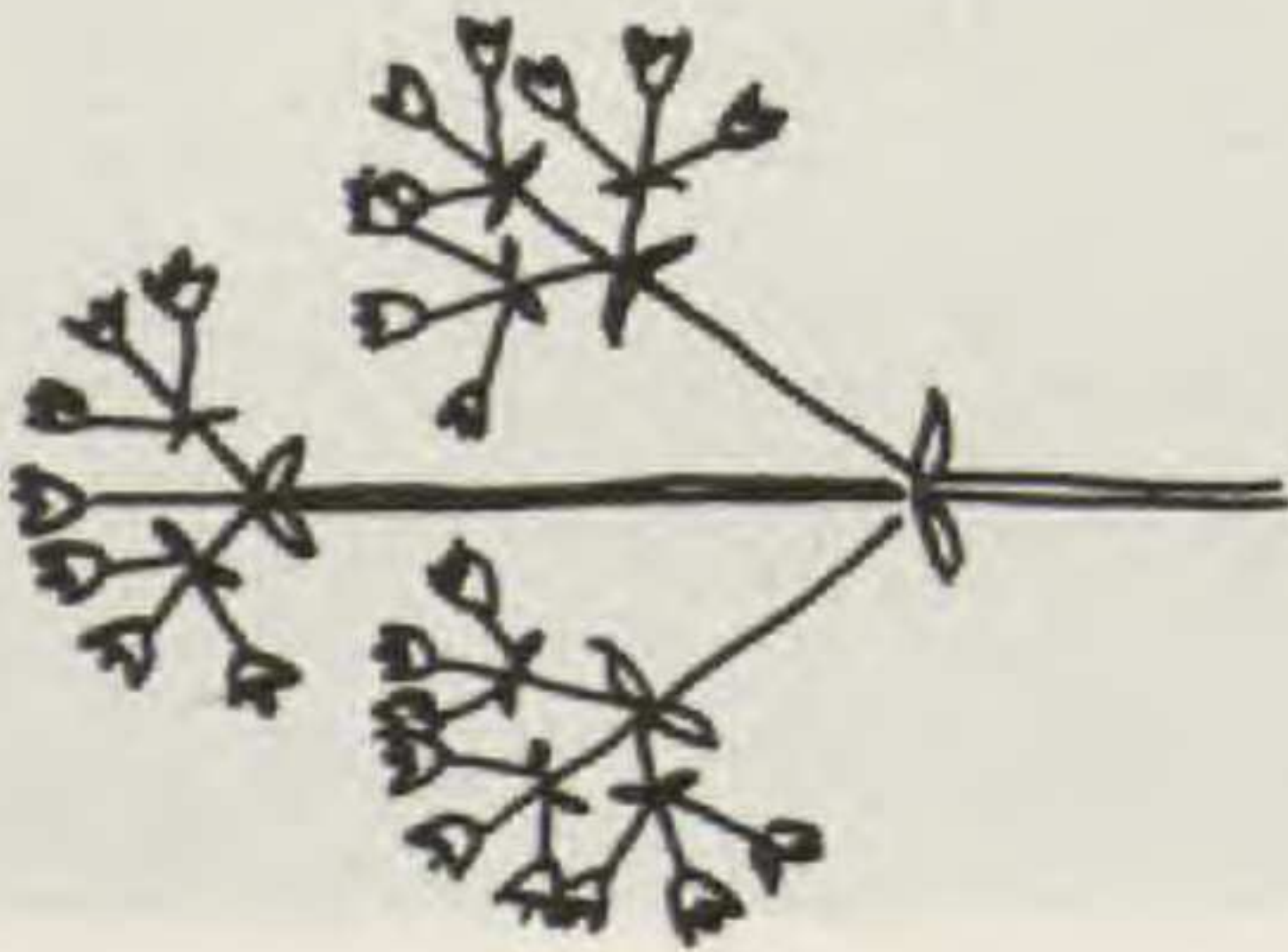
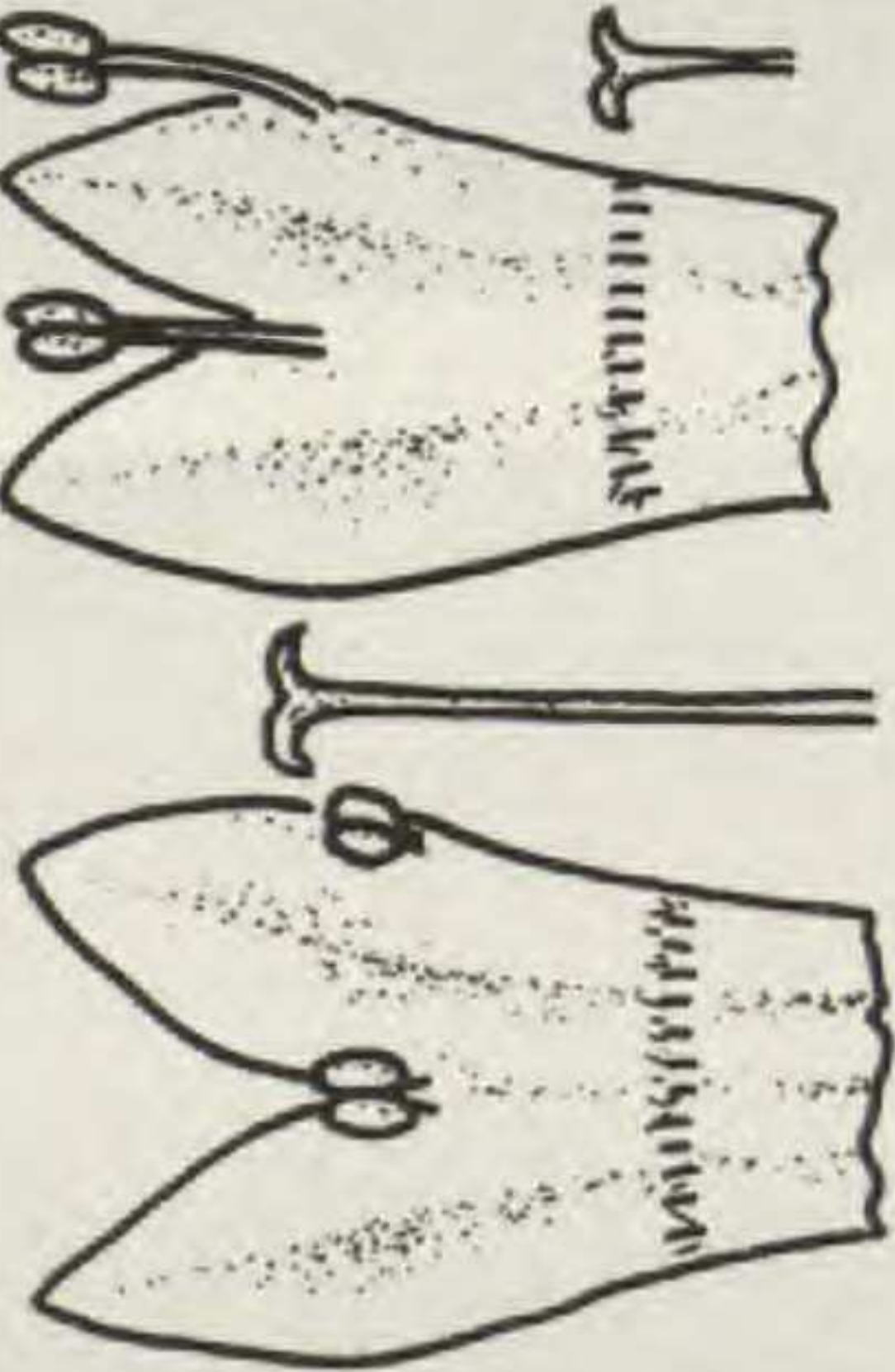
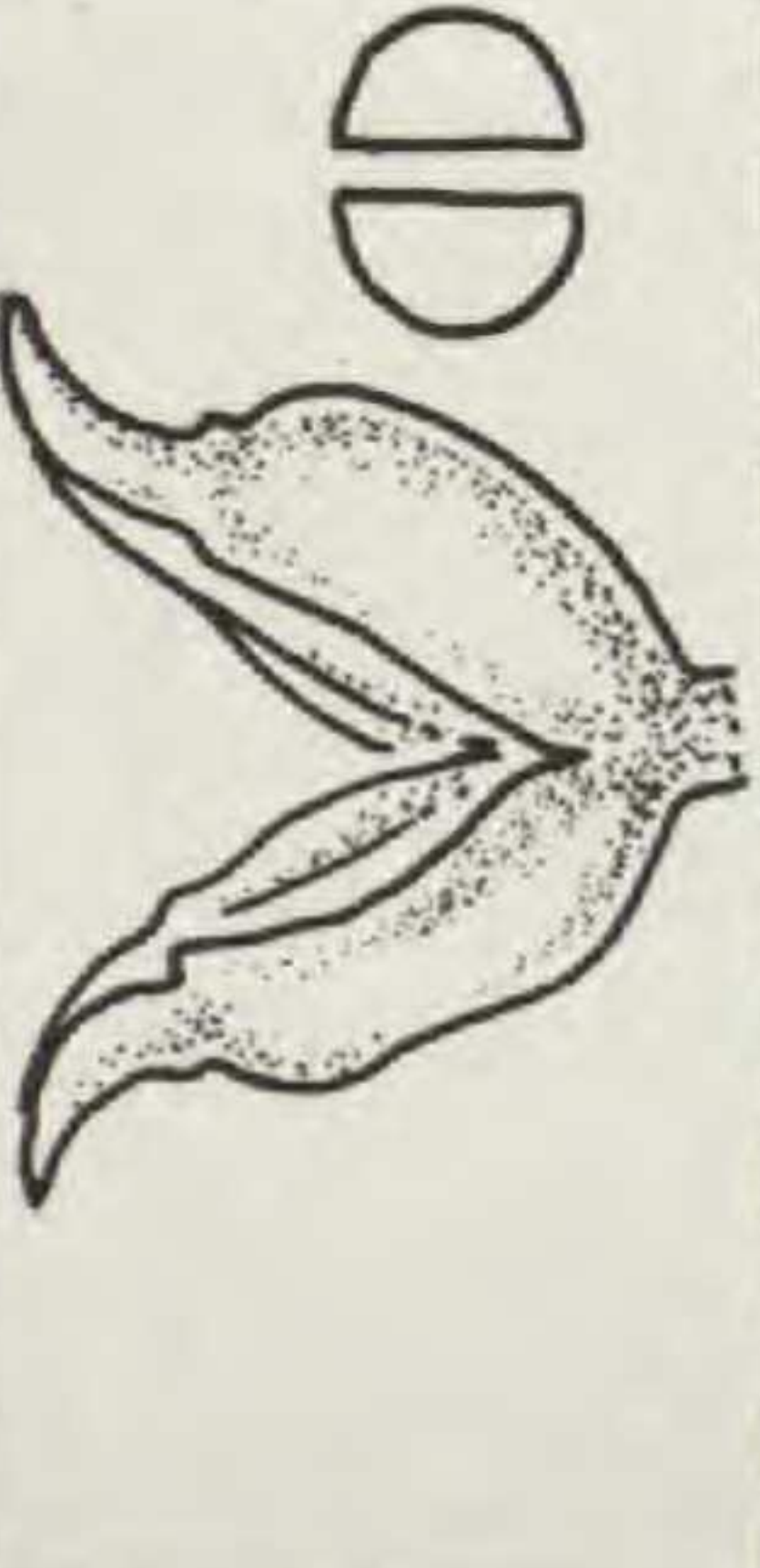
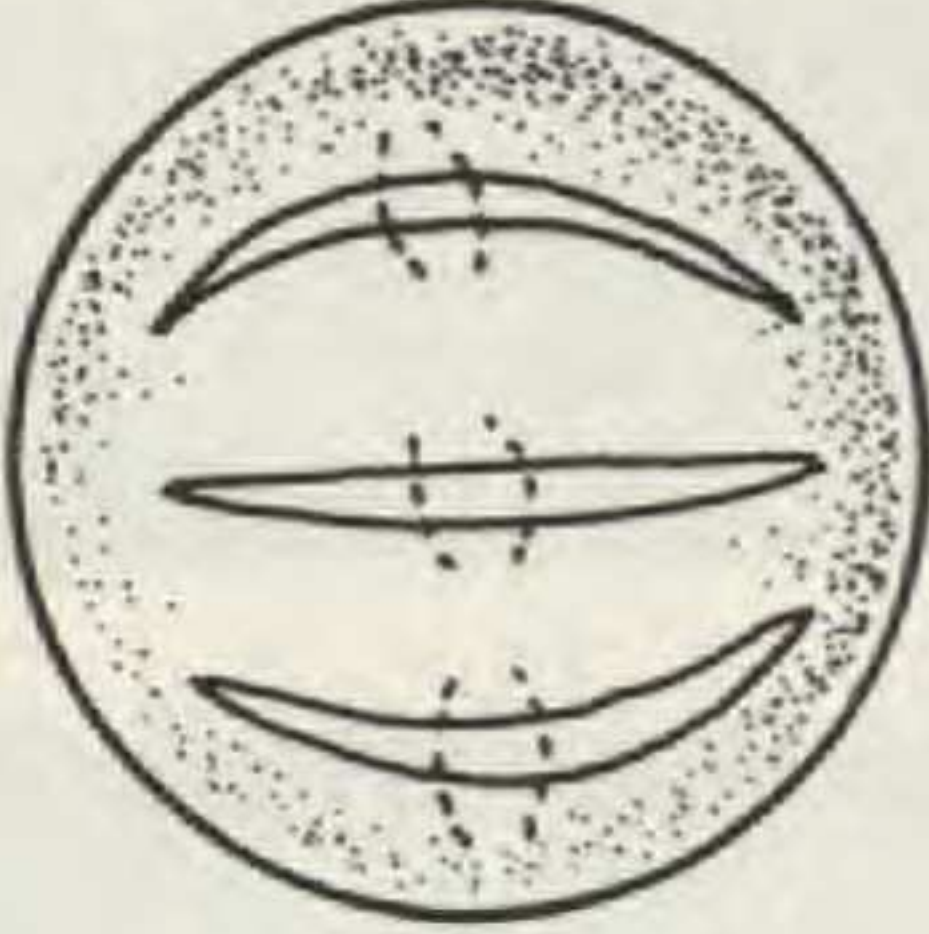

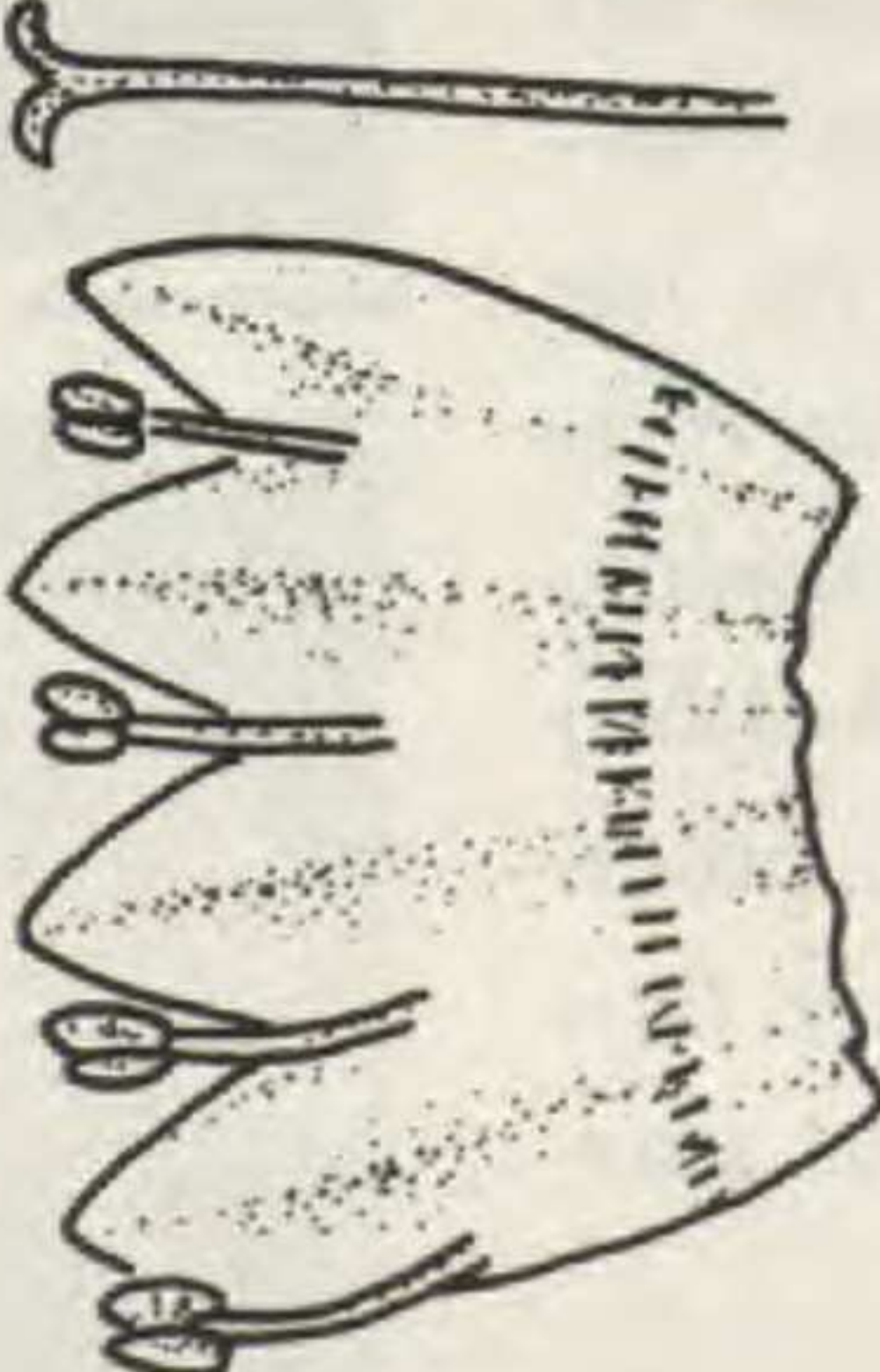
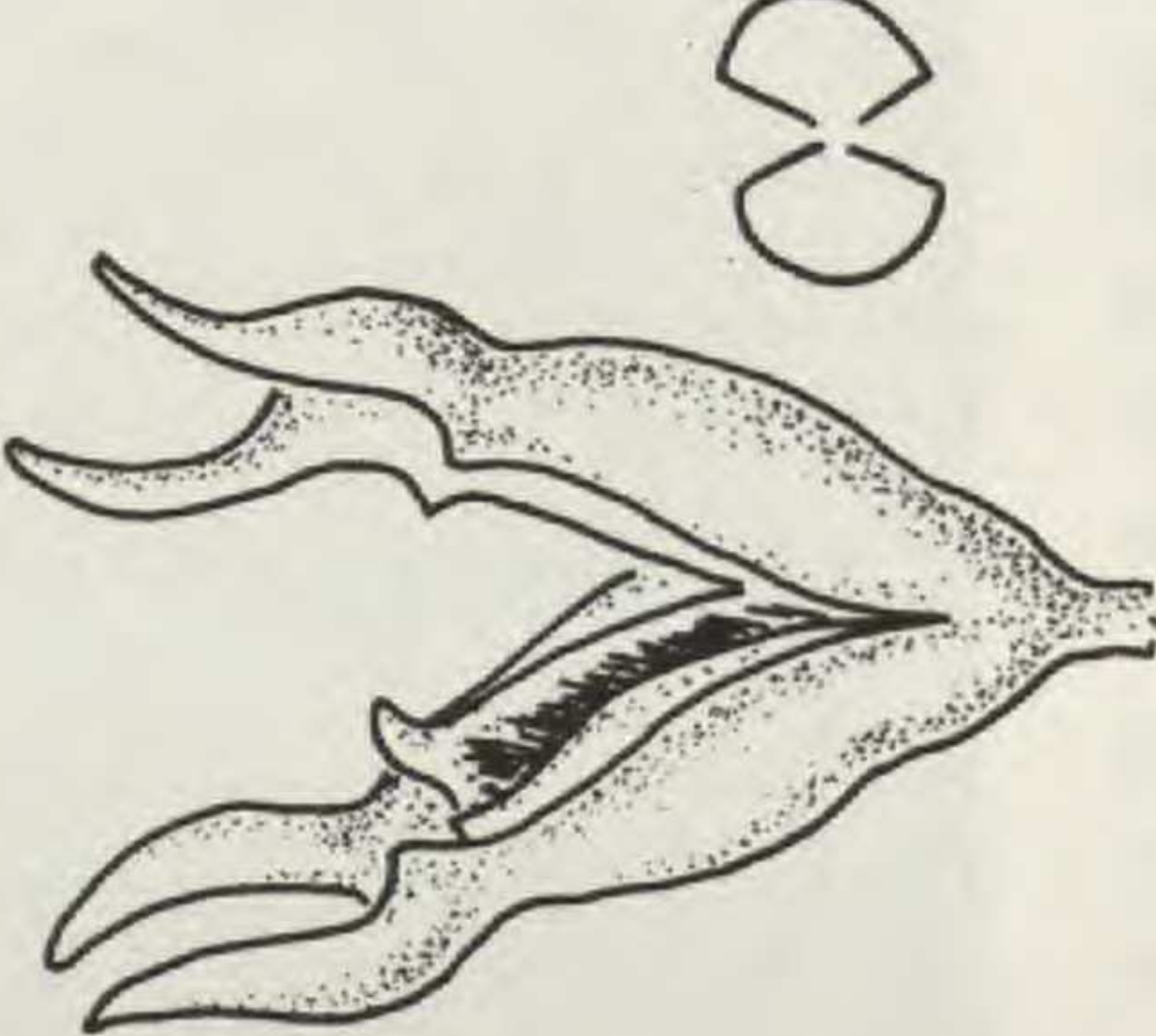
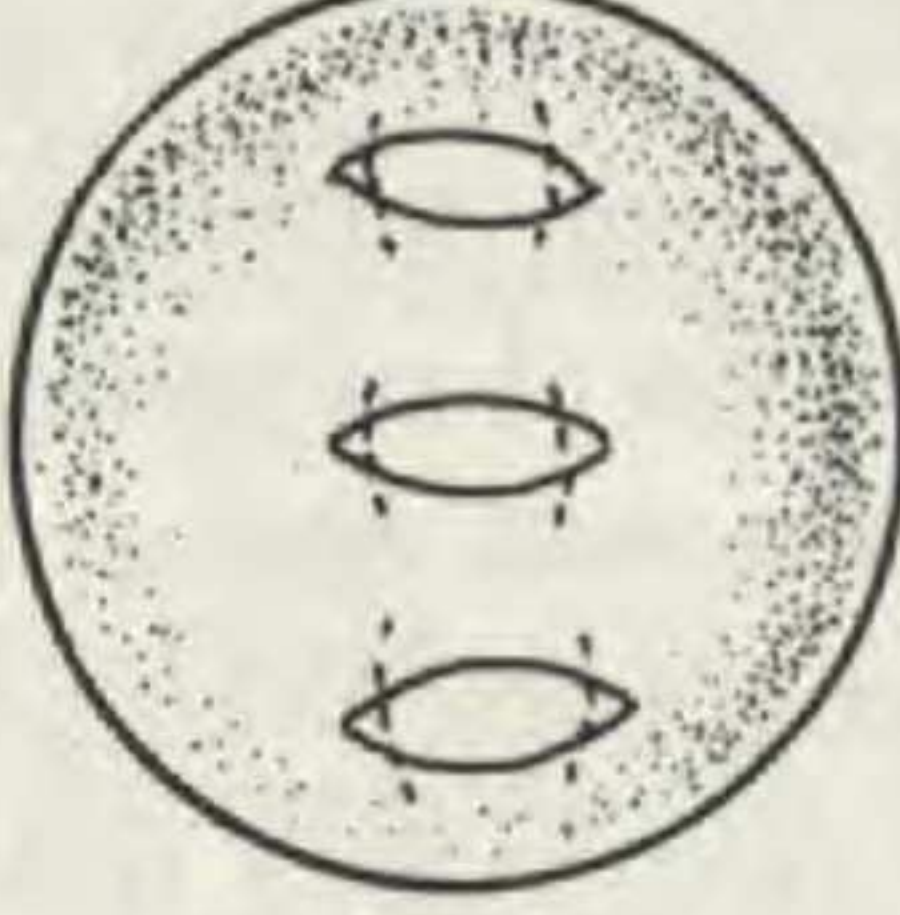

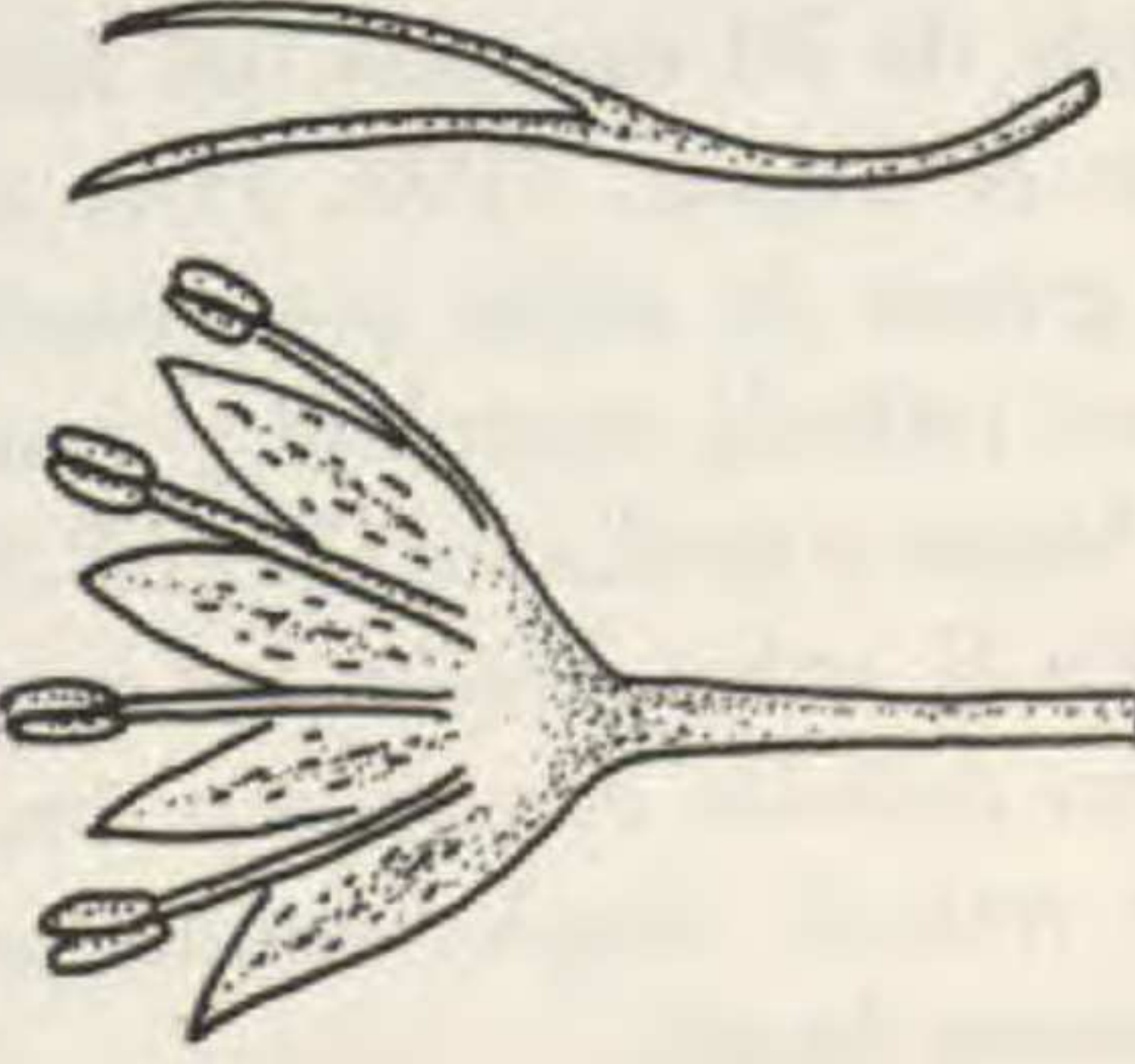
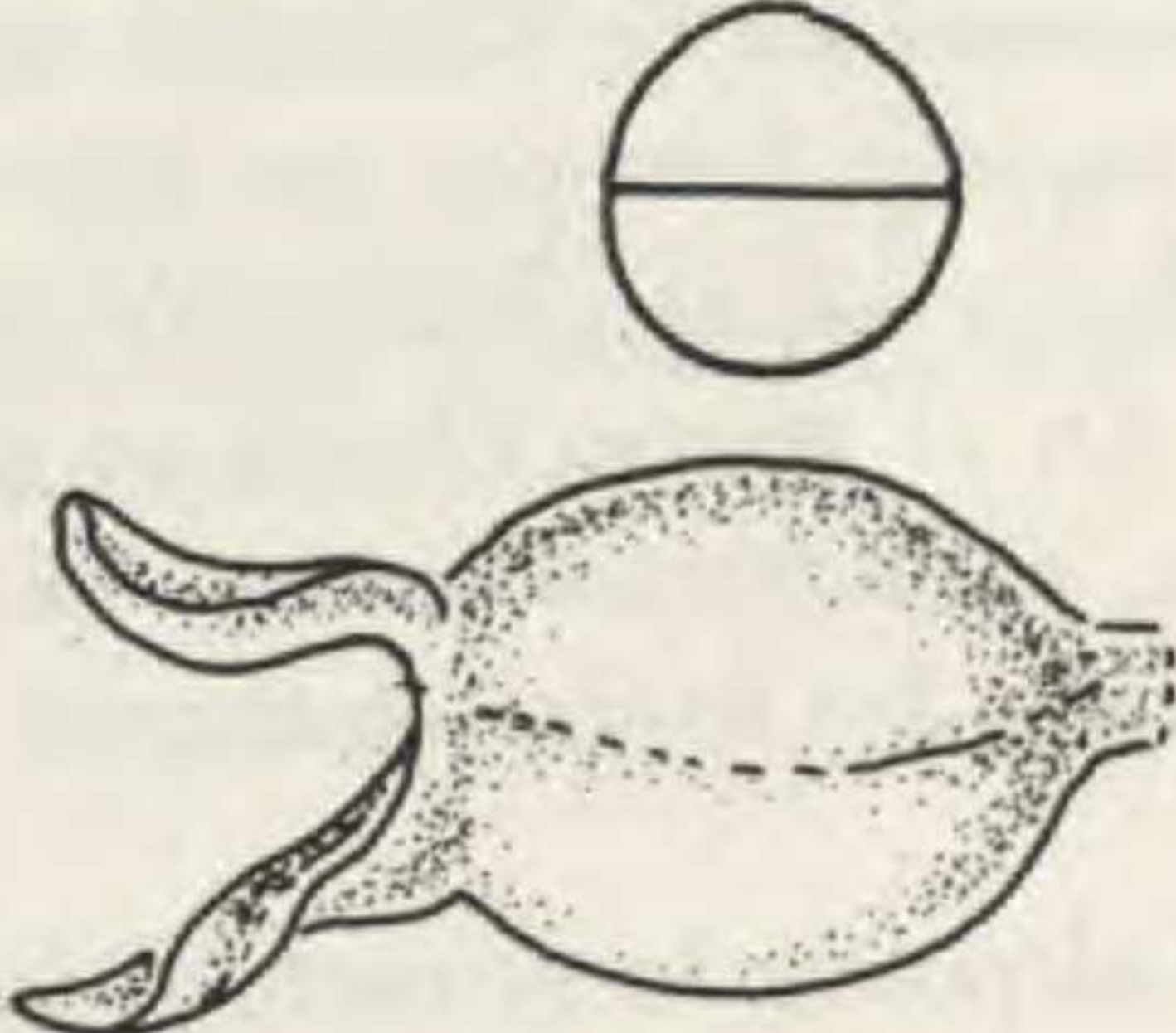
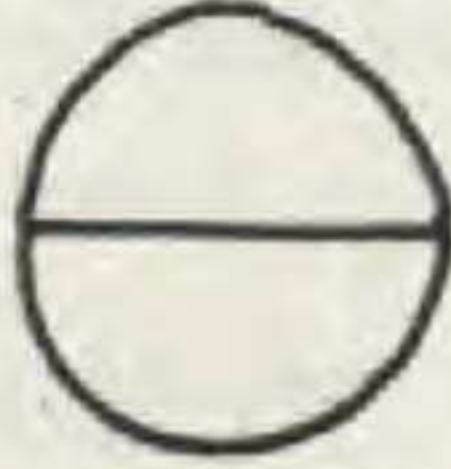
				Sect. Ebelia -- -- GALIANTHE Griseb. Sect. Galianthe
				BORRERIA G.F.W. Meyer
				DIODIA L.

Figura 5. Diferencias y afinidades entre los géneros *Galianthe*, *Borreria* y *Diodia* s. str. sobre la base de sus caracteres exomofológicos (inflorescencia, flor y fruto) y sus caracteres palinológicos. Ver explicación en el texto.

lia y subg. *Galianthe*), *Borreria* y *Diodia* s. str.³, que se consideran de mayor valor taxonómico:

- (1) tipo de inflorescencia: tirsoide, con inflorescencias parciales \pm congestas o empobrecidas, cimoides versus glomeriforme o sólo de 1–2–3 flores;
- (2) tipo de flor: heterostila (longistila y brevistila) versus homostila;
- (3) tipo de fruto: parcial o totalmente dehiscente versus indehiscente;
- (4) tipo de polen: semitectado-reticulado, con colpos largos versus tectado-perforado con colpos cortos.

Como se puede apreciar, en las especies del género *Galianthe*, las inflorescencias son terminales y tirsoides y las flores heterostilas. En el subgénero *Galianthe* se agrupan las especies con frutos de mericarpos dehiscentes y en el subgénero *Ebelia* se reúnen las que tienen frutos de mericarpos indehiscentes. En el género *Borreria* las especies presentan frutos como los de *Galianthe* subg. *Galianthe*, pero se separan bien por sus flores homostilas y por sus inflorescencias glomeriformes, terminales y/o axilares. En el género *Diodia* s. str. las flores son isomorfas, axilares, solitarias o en inflorescencias paucifloras y los frutos totalmente indehiscentes.

En cuanto al polen, la estructura de la exina es el carácter más importante para distinguir *Galianthe* de los otros dos géneros; en segundo lugar se encuentra la longitud de los colpos (Fig. 6).

En *Galianthe* se ha estudiado la morfología del polen de más de 30 especies del subgénero *Galianthe* (Pire & Cabral, 1992; Pire, inéd.) en las cuales los granos de polen son semitectados-reticulados, con retículo complejo y zonocolporados, con colpos largos o medianos ($ECA/P = 0.40\text{--}0.65$) (Fig. 6A). En *G.* subg. *Ebelia*, los granos de polen presentan un retículo complejo o, con menor frecuencia, un retículo simple, siendo los colpos predominantemente largos.

En *Borreria* se analizaron cerca de 50 especies (Cabral, 1985; Pire, inéd.⁴) que presentan gran variabilidad en sus caracteres palinológicos; sin embargo la estructura de la exina, tectada-perforada, se mantiene casi constante en todas ellas. En este género los granos de polen pueden ser colporados o porados; cuando son colporados, los colpos son

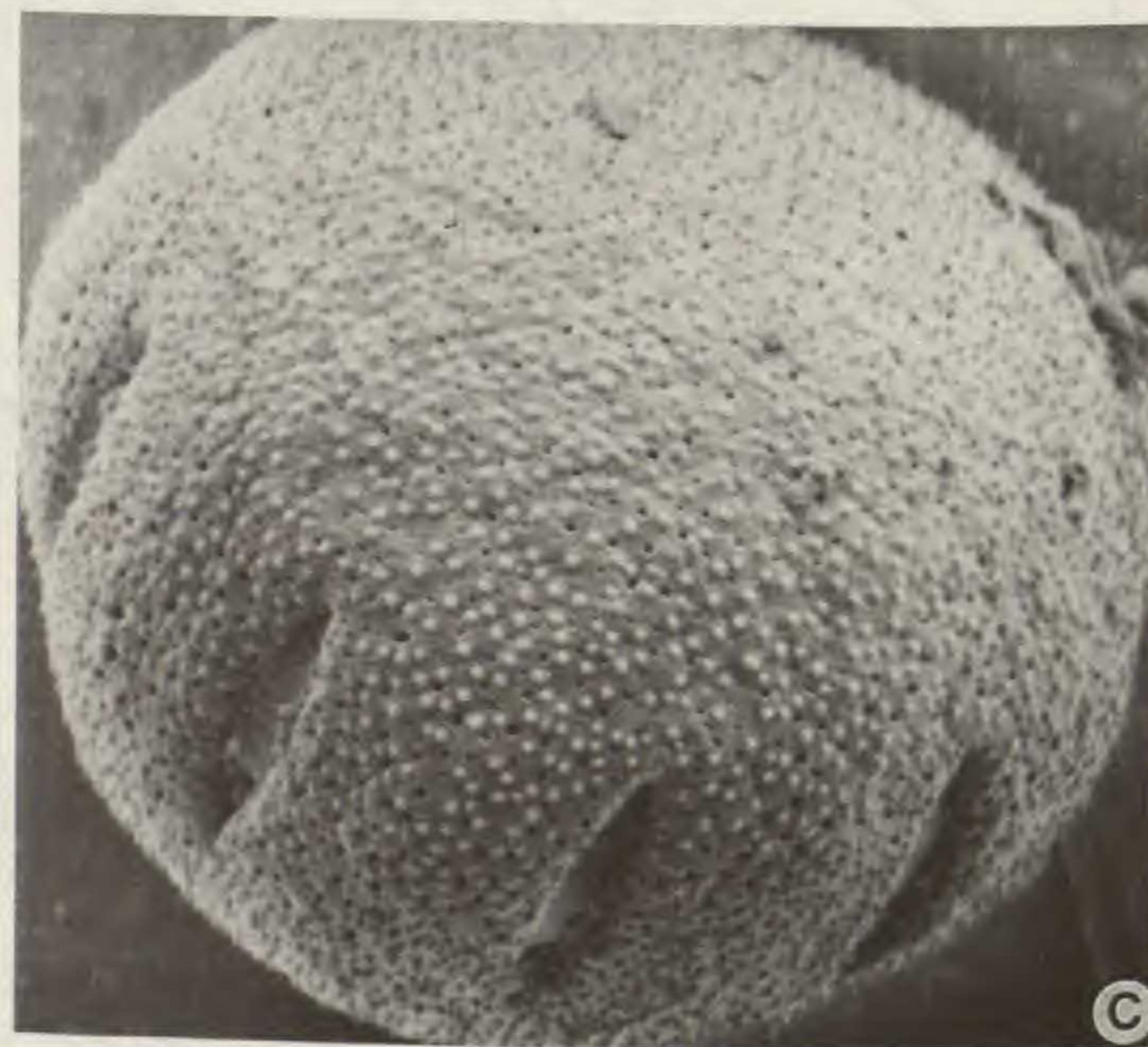
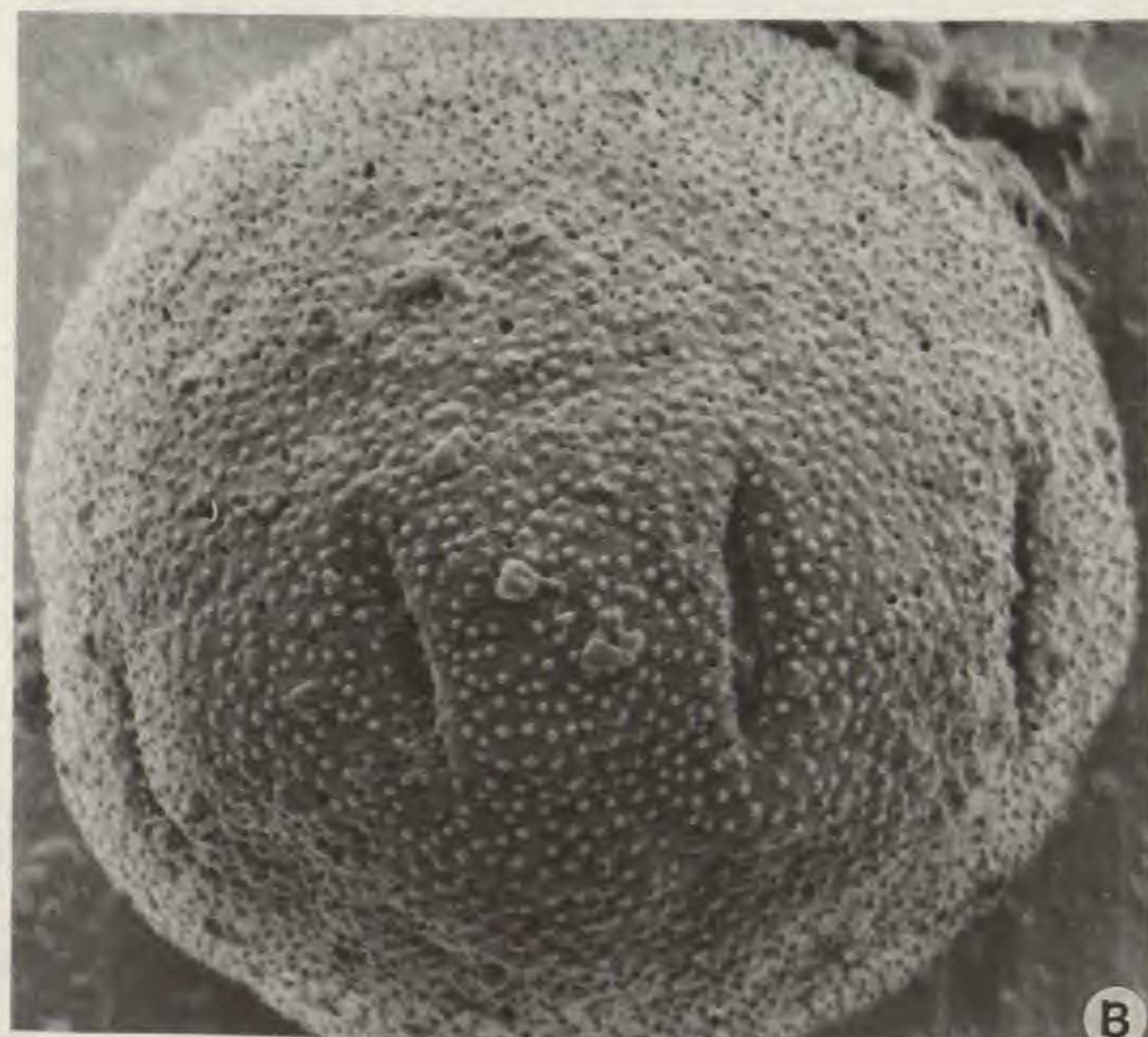
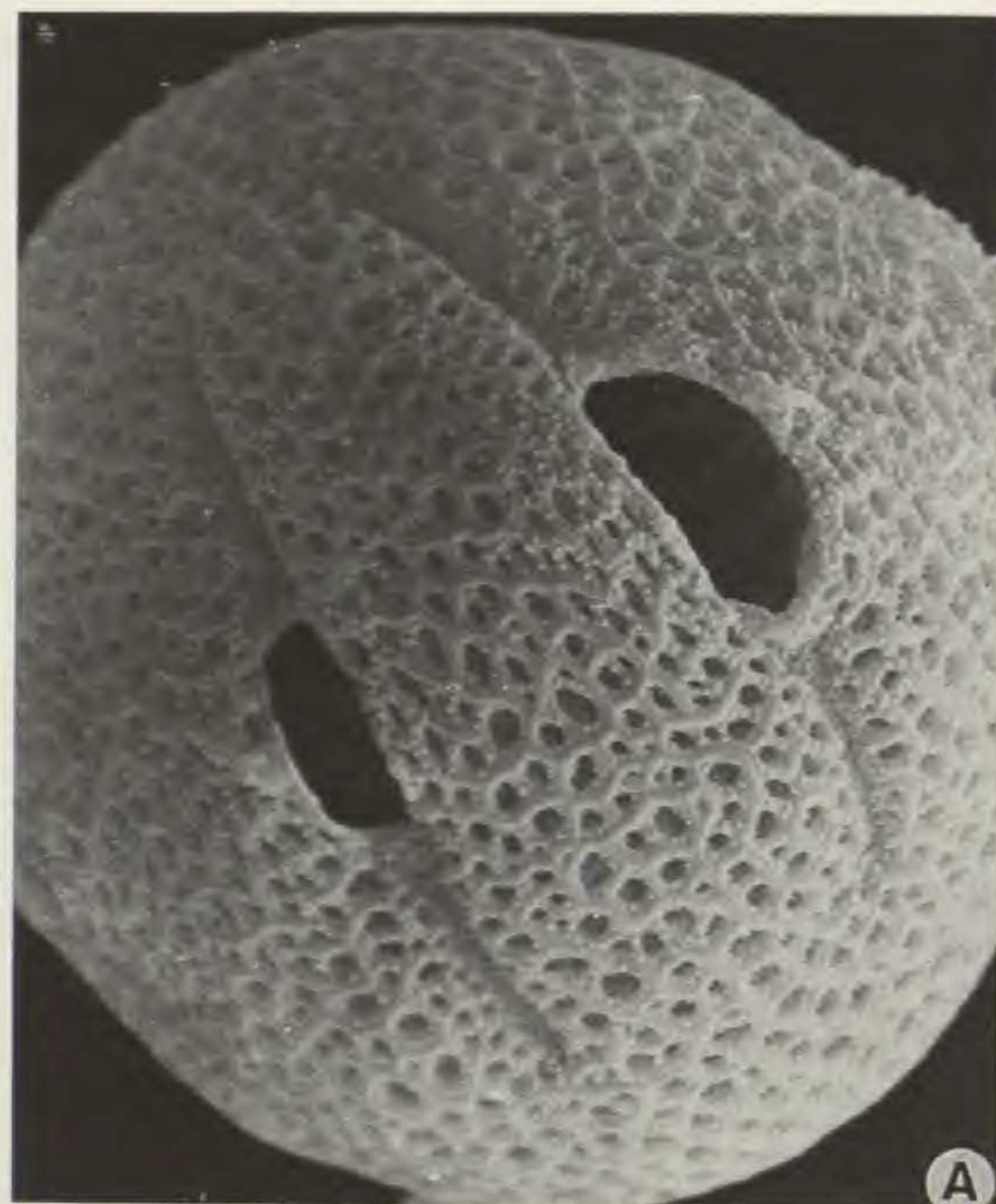


Figura 6. Granos en vista ecuatorial. —A. *Galianthe centranthoides* (flor brevistila). —B. *Borreria terminalis*. —C. *Diodia virginiana*. Las escalas equivalentes a 5 μm .

³ *Diodia* s. str. comprende a las cuatro especies reconocidas por Bacigalupo y Cabral: *D. virginiana* L., *D. kuntzei* K. Schum., *D. macrophylla* K. Schum. y *D. saponariifolia* Cham. & Schldl.

⁴ Trabajo presentado en la II International Rubiaceae Conference, Meise, Bélgica (septiembre, 1995).

generalmente cortos ($ECA/P = <0.35$) (Fig. 6B). Las especies con granos de polen longicolpados poseen exina tectada-foveolada y espínulas localizadas principalmente alrededor de las aberturas.

En cuanto a *Diodia* s. str. (*D. virginiana* L., *D. kuntzei* K. Schum., *D. macrophylla* K. Schum. y *D. saponariifolia* Cham. & Schldl.) posee granos de polen tectado-perforados y con colpos cortos, similares a los ya mencionados para *Borreria* (Fig. 6C).

Con este estudio se demuestra que las especies comprendidas en *Galianthe* subg. *Ebelia* presentan caracteres no sólo exomorfológicos sino también palinológicos que son típicos de *Galianthe*, los que, a su vez, permiten diferenciarlas perfectamente de las de *Borreria* y *Diodia*. Esto apoyaría el criterio de Cabral y Bacigalupo (en este volumen) de ampliar los límites de *Galianthe* creando el nuevo subgénero, *G.* subg. *Ebelia* (Rchb.) E. L. Cabral & Bacigalupo.

Literatura Citada

- Burger, W. & C. M. Taylor. 1993. Rubiaceae, Flora Costaricensis. Fieldiana, Bot. 33: 124.
- Cabral, E. L. 1985. Valor taxonómico del polen en las especies argentinas del género *Borreria* (Rubiaceae). Bol. Soc. Argent. Bot. 24 (1-2): 169-178.
- . 1991. Rehabilitación del género *Galianthe* (Rubiaceae). Bol. Soc. Argent. Bot. 27 (3-4): 235-249.
- & N. Bacigalupo. 1997. Revisión del género *Galianthe* subg. *Ebelia* stat. nov. (Rubiaceae: Spermacoeae). Ann. Missouri Bot. Gard. 84: 857-877.
- Erdtman, G. 1966. Pollen Morphology and Plant Taxonomy. Angiosperms. Haffner, New York.
- Fosberg, F. R., M. H. Sachet & R. L. Oliver. 1981. Rubiaceae. Flora of Micronesia. Smithsonian Contr. Bot. 81, 5: 44-135.
- Galati, B. G. 1991. Estudios embriológicos en la tribu Spermacoeae (Rubiaceae). Parte I: Anatomía floral. Microsporogénesis. Megasporogénesis. Bol. Soc. Argent. Bot. 27 (1-2): 7-20.
- Howard, R. A. 1989. Rubiaceae. Flora of the Lesser Antilles 6 (3): 389-471. Harvard Univ., Jamaica Plain, Massachusetts.
- Kremp, G. O. W. 1968. Morphology Encyclopedia of Palynology. Univ. Arizona Press, Tucson.
- Pire, S. M. & E. L. Cabral. 1992. El valor del polen en la revalidación de *Galianthe* (Spermacoeae-Rubiaceae). Darwiniana 31 (1-4): 1-10.
- Steyermark, J. A. 1974. Rubiaceae: Spermacoeae, Flora de Venezuela 9 (3): 1834-1978. Instituto Botánico, Caracas.
- Verdcourt, B. 1976. Rubiaceae in R. M. Polhill, Flora of Tropical East Africa: 333-380. Agents for Oversea Governments and Admin., London.

THE TANAKA-KAIYONG LINE—AN IMPORTANT FLORISTIC LINE FOR THE STUDY OF THE FLORA OF EAST ASIA¹

Li Xi-wen² and Li Jie²

ABSTRACT

The "Tanaka-Kaiyong Line" is a line separating two floristic subkingdoms of East Asia, the Sino-Japanese to the east and the Sino-Himalayan to the west. It lies in the provinces of Sichuan and Yunnan in China. It is comprised of the "Tanaka Line of *Citrus* Distribution" in Yunnan province and the "Kaiyong Line of Orchid Distribution" in Sichuan province, which nearly connect at the border of NW Yunnan and SW Sichuan. After a survey of the distribution patterns of some genera, we are sure that it exists. The Tanaka-Kaiyong Line is significant not only for the subdivision of the East Asia Kingdom and the floristic regionalization of China, but also for the separation of some critical species and the study of vicariance. Moreover, three important floristic regions, the Hengduan Mountain region, Central China region, and Dian-Qian-Gui region, which are noted for species abundance, endemism, and high speciation, are situated near this Line. Compared with Sino-Himalayan genera, the Sino-Japanese are more completely separated by the Tanaka-Kaiyong Line, possibly due to their different florogenetic backgrounds and different times of origin. Additionally, it seems that the centers of biodiversity (or abundance centers) of Chinese endemic genera on each side of the Tanaka-Kaiyong Line are different. The centers on the west side of the Line are mainly neoendemic, but those on the east are mainly paleoendemic. This difference may be caused by geological-geomorphological patterns and the large-scale climatic conditions in China. The formation of Hengduan Mountain and Yunnan Plateau, which was induced by the uplifting of the Himalayas, greatly affected the floristic nature of western East Asia and, therefore, the floristic distributions that led us to define the Tanaka-Kaiyong Line have probably arisen since that time.

Recently in the study on the flora of East Asia it was noted that an important floristic line exists in the western part of East Asia. This line is important in the understanding of the characteristics and biodiversity of the East Asian flora.

I. WHAT IS THE TANAKA-KAIYONG LINE?

The Tanaka-Kaiyong Line is named for the "Tanaka Line" in Yunnan province and the "Kaiyong Line" in Sichuan province. These two lines almost connect at the border of NW Yunnan and SW Sichuan and act as a dividing line between Sino-Japanese and Sino-Himalayan genera.

The Tanaka Line was first suggested by the Japanese scholar Tyôzaburô Tanaka (Tanaka, 1954) in the treatment of the taxonomy and distribution in *Citrus*. Tanaka discovered that a line can be drawn in between the two groups of chains (*Metacitrus* predominating and *Archicitrus* predominating) that is significant in distinguishing the mode of distri-

bution of citrus fruit. This line might be called the "Tanaka Line of *Citrus* Distribution" in connection with the natural development of the *Citrus* flora of the Far East. The approximate position of the Tanaka Line can be shown as a straight line starting at the intersection of 28°N, 98°E southward to approximately 18°45' or 19°N, 108°E. Tanaka tested the existence of this line by plotting the distribution of the genera in Aurantioideae. Of a total of 22 genera in continental Asia, 10 (45%) do not occur east of the Tanaka Line, while 1 (*Poncirus*) stays inward, totaling 11 genera (50%) that stop at this line. Likewise, a great number of Indo-Malayan plant families stop at this line, as does the westward advance of Sino-Japanese plant families.

The "Kaiyong Line" was first suggested by the Chinese scholar Lang Kaiyong (Lang, 1994) as a line separating the Sino-Himalayan and Sino-Japanese subkingdoms in Sichuan Province. It is based on the distribution patterns of some genera or subgenera of Orchidaceae typical for these two

¹ Dedicated to our advisor, Wu Zheng-yi (Wu Cheng-yih). We congratulate him on his 80th birthday and his great achievements in botanical research, in which he has been engaged for 60 years. We also thank him for his years of tireless teaching. This paper is one of the research reports of the project of "The floristic study on the Chinese seeds plants" (9390010), which was financed by the NSFC. We thank Diana (Nan) Winkelmeyer of the Missouri Botanical Garden for editorial help with the manuscript.

² Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, Yunnan 650204, People's Republic of China.

subkingdoms because the family is more restricted by environmental conditions than other families. The Sino-Himalayan genera are *Risleya*, *Diplomeris*, *Diphylax*, *Platanthera* subg. *Stigmatosa*, and the Sino-Japanese are *Neofinetia*, *Vexillabium*, and *Sedirea*. The Kaiyong Line runs north to south as: Naping (Jiuzhaigou), Songpan (Huanglongzhi), Maowen, Guanxian (Guangguanshan), Baoxing, Erlangshan (west of Tianquan), Emei Mountain, Shimian, Xichang, Dechang, Miyi to Panzhihua City. This line is not named by Lang. We named this line the "Kaiyong Line of Orchid Distribution" because Lang was the first person to suggest the line in W Sichuan in the literature and in relation to the Tanaka Line. We have treated the Kaiyong Line as a northern extension of the Tanaka Line because the two are nearly connected, and both act as dividing lines between Sino-Japanese and Sino-Himalayan genera.

II. SIGNIFICANCE IN FLORISTIC STUDY

The Tanaka-Kaiyong Line as a dividing line in the flora of East Asia is of great significance in floristic study. It is characterized by the following:

1. IT ACTS AS A DEMARCATION FOR THE SUBDIVISION OF THE EAST ASIA KINGDOM.

Recently many Chinese scholars have suggested East Asia as a floristic Kingdom in the floristic regionalization of the world, because East Asia has no less than 30 endemic families and 577 endemic genera (excluding the Pteridophytes) [according to Wu (1993), but according to Takhtajan (1986), it has more than 20 endemic families and over 300 endemic genera]. In addition, East Asia has a high level of endemic species. The area that comprises Wu's "Sino-Japanese" region is almost the same as the East Asia Kingdom. East Asia borders on the Pacific Ocean with a broad east side and a narrow west side (Fig. 1). It is floristically closely related to the Holarctic Kingdom in the north and the Palearctic Kingdom in the south. The East Asia Kingdom can be divided into two subkingdoms, the Sino-Japanese in the east and Sino-Himalayan in the west. The floras of these subkingdoms exhibit vicariance between eastern and western taxa, with the line of demarcation situated in western East Asia. The Tanaka-Kaiyong Line evidently divides these two subdivisions on the whole. Because the Line is based on the distribution patterns of the Sino-Japanese genera and the Sino-Himalayan genera, it is of great significance for the subdivision of the East Asia Kingdom floristically, and also for the floristic regionalization of China. Moreover, three

important floristic regions are situated near this line: the Hengduan Mountain region on the west and the Central China and Dian-Qian-Gui regions on the east. These three regions have a great abundance of species, the highest levels of endemism at the specific level and speciation in China (Li, 1996).

2. IT HELPS THE SEPARATION OF SOME CRITICAL SPECIES AND THE STUDY OF VICARIANCE.

Because the Tanaka-Kaiyong Line divides the Sino-Japanese and Sino-Himalayan floras, it is helpful in the delineation of some critical species belonging to these two floras. The species endemic to one flora are quite different from those endemic to the other, because the floras have different speciation in time and space. For example, *Cyclobalanopsis glauca* (Thunb.) Oerst. of the Sino-Japanese flora is different from *C. glaucoides* Schott. of the Sino-Himalayan flora, although they are very similar morphologically. The concept of the Tanaka-Kaiyong Line helps in separating the species according to their distribution patterns. Vicariance is an important problem in phytogeographical study, and is evident in China between eastern and western taxa, not only for the oaks, conifers, and other evergreen or deciduous trees at low altitudes, but also for hemlocks and firs at high altitudes. For example, *Pinus yunnanensis* Franch. of W China is a vicariant species of *P. massoniana* Lamb. of E China, *Keteleeria evelyniana* Mast. of *K. davidiana* (Bertr.) Beissn., *Castanopsis delavayi* Franch. of *C. sclerophylla* (Lindl.) Schott., *Cyclobalanopsis delavayi* (Franch.) Schott. of *C. gilva* (Bl.) Oerst., *Alnus nepalensis* D. Don of *A. crematogyne* Burkill, and so on. The concept of the Line, together with an analysis of phylogeny, will lead to a determination of what is true and what is false vicariance. It seems that the Line is helpful in the study of the vicariance between the Sino-Himalayan and Sino-Japanese floras.

3. IT FACILITATES UNDERSTANDING OF THE SINO-JAPANESE AND THE SINO-HIMALAYAN ELEMENTS.

After surveying distribution patterns of some genera in both the Sino-Japanese and the Sino-Himalayan floras (Li & Li, 1992), we are sure that the Tanaka-Kaiyong Line is real. In comparison with the Sino-Himalayan genera, the Sino-Japanese genera follow the line more strictly, perhaps because of their different florogenetic backgrounds and different origin times. In general, the Sino-Himalayan elements are younger and more dynamic, so they do not conform as strictly to the Line,

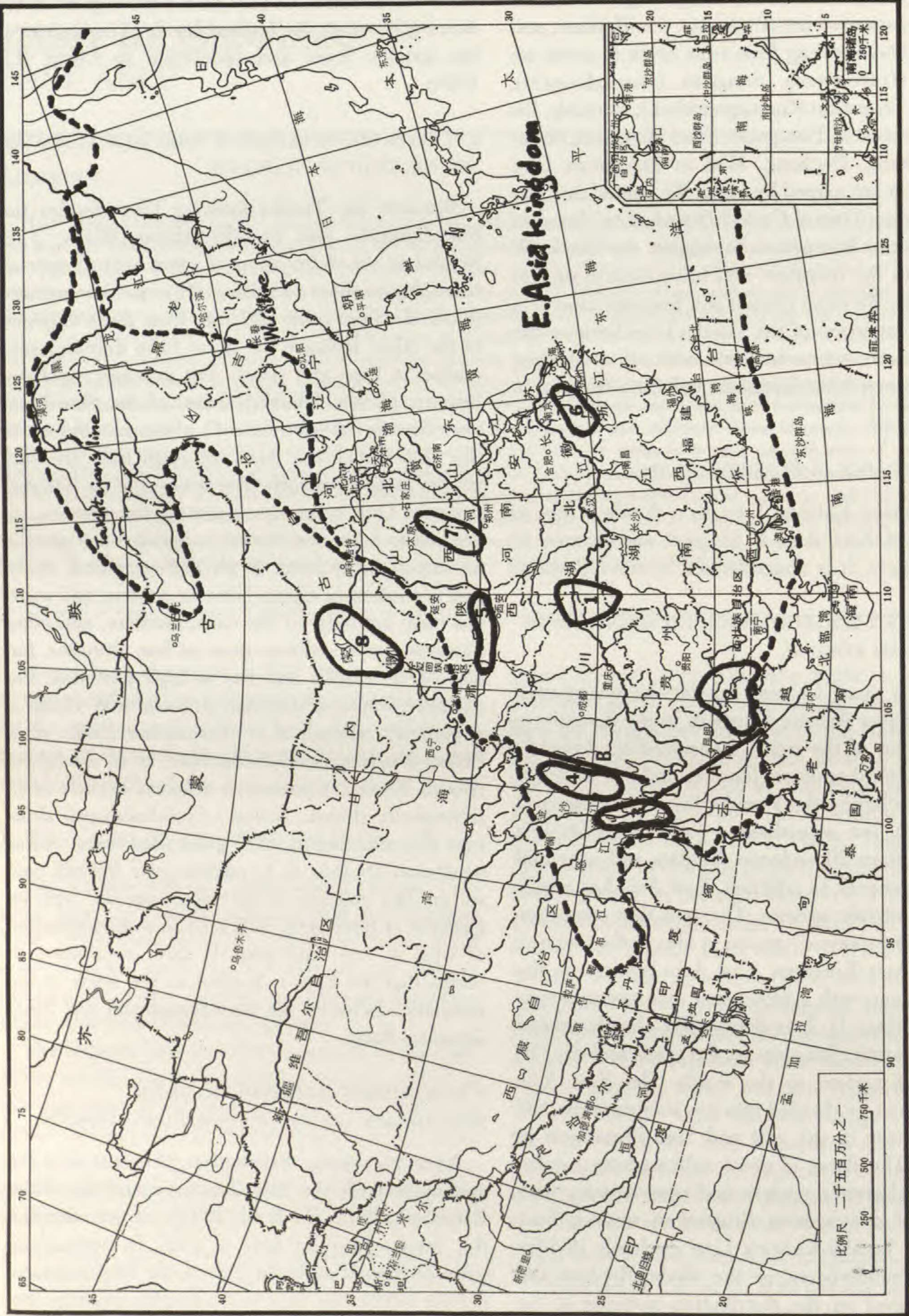


Figure 1. A sketch map of the Tanaka-Kaiyong Line and the centers of biodiversity (or abundance centers) of Chinese spermatophytic endemic genera. Tanaka-Kaiyong Line: A. Tanaka Line; B. Kaiyong Line. Biodiversity centers (or abundance centers) of Chinese spermatophytic endemic genera: 1. Mid-Yangtze center; 2. Dian-Qian-Gui center; 3. South Hengduan Mountain center; 4. Middle Hengduan Mountain center; 5. Qingling center; 6. Huangshan-Tianmushan center; 7. Zhongtiao-South Taihangshan center; 8. South Inner Mongolia center. [Note: Wu's northern border of East Asia is lower than that of Takhtajan (1986).]

and the Sino-Japanese elements are relict, so they conform more strictly to it. This conclusion is in accordance with Wu: "From the florogenetic point of view, the genera of the Sino-Japanese distribution pattern are usually epibiotic and relict in nature, being the historical elements from an ancient Laurasian flora, while the Sino-Himalayan are mixed with several neoendemic elements derived from both Laurasian, Tethyan and Gondwanic elements. The Tethyan origin shows especially in such families as Apiaceae, Boraginaceae, Brassicaceae, Dipsacaceae, Lamiaceae, etc. Probably it implies that the Sino-Japanese distribution pattern is older than the Sino-Himalayan distribution pattern, and also implies that the degree of diversification is stronger and more progressive in Sino-Himalayan flora."

4. IT AIDS THE UNDERSTANDING OF BIODIVERSITY CENTERS (OR ABUNDANCE CENTERS) OF CHINESE ENDEMIC GENERA.

We noted that the centers of biodiversity (or abundance centers) of Chinese endemic genera on each side of the Tanaka-Kaiyong Line are quite different, those west of the Line being mainly neoendemic and those east mainly paleoendemic. According to Ying and Zhang (1984) the west side of the Line has one center of biodiversity, W Sichuan-NW Yunnan, but according to Wang and Zhang (1994) there are two centers, the South Hengduan Mountain center and Middle Hengduan Mountain center. Ying and Zhang's concept of the east side of the Line has two centers, SE Yunnan-W Guangxi and E Sichuan-W Hubei, while Wang and Zhang's concept (Fig. 1) has six: Mid-Yangtze, Dian-Qian-Gui, Qingling, Huangshan-Tianmushan, Zhongtiao-South Taihangshan, and South Inner Mongolia. We think the South Inner Mongolia center, unlike the others, is mainly dry desert, and that Qingling is not a center in a strict sense because it has no endemic genera but supports Chinese endemic genera shared with other regions, especially with Central China (Ying, 1994); thus the east side of the Line has a maximum of four centers in the strict sense for the East Asia Kingdom. Therefore, the different natures of the centers on both sides of the Line are parallel with those of the elements on both sides of the Line. The cause of the difference between the centers of biodiversity on either side of the Line may be directly related to geological-geomorphological patterns and large-scale climatic conditions in China. The area on the west side of the Line is situated on the transitional site from the second to the first terraces geomorphologically and

climatically affected by monsoons from both the Indian and Pacific Oceans, while the area on the east side is on the site from the third terrace, or coast land, to the second terrace geomorphologically, and is climatically affected mainly by the monsoons from the Pacific Ocean.

III. ORIGIN OF THE FLORISTIC LINE

The Tanaka-Kaiyong Line, which divides two subkingdoms of the East Asia Kingdom, is a result of the large-scale geological-geomorphological patterns in China, as already mentioned above. Liu and Ding (1984) summarized the history of the geological structure of China. The main Chinese platform had risen above the sea by the end of the Triassic, except that some residual epi-continental waters remained, including one over present-day Yunnan. A trough also extended across what is now the Qinghai-Xizang plateau north of the present Himalayas. From the end of the Jurassic-Cretaceous, a sequence of underthrusts from the south extended the continental land area of China southward and raised the whole platform, particularly in the west. By the end of the Paleocene the present outline of continental China had become established, except that the Himalayan region remained marine until the Eocene. The Himalayas were the product of northward underthrusting of the Indian Plate (Chang & Pan, 1981) and only came into being as a mountain range late in the Cenozoic, or perhaps in the Miocene-Pliocene. It seems that uplift took place at an accelerating rate. The average for the 3000 m rise during the Quaternary is 1.5 mm per year, but the rise during the Holocene may have been four or five times greater (Xu, 1984). The great uplifting of the Himalayas induced the rising and the climatic fluctuation of Henguan Mountain and the Yunnan Plateau, and also greatly affected the floristic nature of the west of East Asia, and the Tanaka-Kaiyong Line thus appeared since that time.

Literature Cited

- Chang C. & Pan Y. 1981. A brief discussion on the tectonic evolution of Qinghai-Xizang plateau. Pp. 1-18 in Liu D. S. (editor), *Geological and Ecological Studies of Qinghai-Xizang Plateau*. Volume 1. Science Press, Beijing.
- Lang K. Y. 1994. Studies on the distribution patterns of some significant genera in orchid flora. *Acta Phytotax. Sin.* 32: 328-339.
- Li X. W. 1996. Floristic statistics and analyses of seed plants from China. *Acta Bot. Yunnan.* 18(4): 363-384.
- Li X. W. & Li J. 1992. On the validity of Tanaka Line and its significance viewed from the distribution of eastern Asiatic genera in Yunnan. *Acta Bot. Yunnan.* 14(1): 1-12.

- Liu T. S. & Ding M. L. 1984. The characteristics and evolution of the palaeoenvironment of China since the late Tertiary. Pp. 11–40 in R. O. Whyte (editor), *The Evolution of the East Asian Environment, Volume I*. Center of Asian Studies, Univ. Hong Kong.
- Takhtajan, A. 1986. Pp. 39–78 in *Floristic Regions of the World*. Univ. California Press, Berkeley, Los Angeles, and London.
- Tanaka, T. 1954. Species problem in *Citrus*. Pp. 58–69 in *Japanese Society for the Promotion of Science*, Ueno, Tokyo.
- Wang H. S. & Zhang Y. L. 1994. The biodiversity and characters of spermatophytic genera endemic to China. *Acta Bot. Yunnan*. 16: 209–220.
- Wu C. Y. 1993. Delineation and unique features of the Sino-Japanese Floristic region.—A speech at the XV International Botanical Congress, Tokyo.
- Xu R. 1984. Changes of the palaeoenvironment of southern east Asia since the late Tertiary. Pp. 419–425 in R. O. Whyte (editor), *The Evolution of the East Asian Environment, Volume II*. Center of Asian Studies, Univ. Hong Kong.
- Ying T. S. 1994. An analysis of the flora of Qingling mountain range: Its nature, characteristics and origin. *Acta Phytotax. Sin.* 32(5): 389–410.
- Ying T. S. & Zhang Z. H. 1984. Endemism in the flora of China—Studies on the endemic genera. *Acta Phytotax. Sin.* 22(4): 259–268.

CHROMOSOME NUMBERS IN COMPOSITAE, XVII: SENECIONEAE III¹

Harold Robinson², Gerald D. Carr³,
Robert M. King², and A. Michael Powell⁴

ABSTRACT

A brief review is offered of major chromosome number variations in the Senecioneae based on recent delimitations of the tribe. An additional 78 chromosome reports are provided, including 19 new reports for species, with confirmed or expanded base numbers for the genera *Gynoxys* ($x = 40$), *Lasiocephalus* ($x = 20$), *Pentacalia* ($x = 20$, ca. 50), and *Jessia* ($x =$ ca. 50). The base number for the tribe is $x = 10$, which is found in various multiples. The Blennospermatinae are one of the most distinct groups with a base of $x = 9$, considered an aneuploid reduction from $x = 10$. A new subtribe, Abrotanellinae, is established for the southern South American and southwest Pacific genus *Abrotanella*, which also has $x = 9$ and has often been placed in the Blennospermatinae. Numbers based on $x = 30$ and aneuploid reductions are found in the Tussilagininae, in many Australian *Senecio*, and in the Macaronesian *Pericallis* of the Senecioninae. The origin of such numbers is discussed. An anomalous North American group of *Senecio* (*Packera*) has variable numbers mostly near $n = 23$. Most Western Hemisphere Senecioninae have numbers of $n = 20$ or multiples thereof, with higher numbers in many Andean groups. Numbers of $n = 10$ or lower are mostly restricted to the Eastern Hemisphere, and groups like *Emilia* have recently dispersed from that area. Occurrences of $n = 5$ in *Emilia*, $n = 10$ in some American and Australian *Senecio*, and $n = 14$ –16 in some tussilaginooids are considered as reductions.

This paper continues a series dealing with chromosome numbers of Compositae (Raven et al., 1960; Raven & Kyhos, 1961; Ornduff et al., 1963, 1967; Payne et al., 1964; Solbrig et al., 1964, 1969, 1972; Anderson et al., 1974; Powell et al., 1974, 1975; King et al., 1976; Tomb et al., 1978; Robinson et al., 1981, 1985, 1989). This is the third of the series ostensibly dealing with the tribe Senecioneae. It presents an updated summary of the chromosome numbers in the tribe (Appendix 1) and 78 new reports of chromosome numbers, including 19 previously uncounted species listed below in the results (Table 1). The new counts are particularly important in some of the less well known neotropical genera such as the Central American *Jessia* and the Andean *Gynoxys*, *Lasiocephalus*, and *Pentacalia*. Nevertheless, the new counts are not considered to be as important in this paper as the overview of the chromosome number patterns in the tribe, to the extent that they are presently known.

The limits of the Senecioneae in the present paper are in the newer, more restricted sense (Bremer, 1994), following more closely the studies of Nordenstam (1977), Jeffrey et al. (1977), and Jeffrey

(1979) and are essentially those of Jeffrey (1992). Previous studies in the present series (Ornduff et al., 1963, 1967), treating the Senecioneae, used the apophyletic traditional concept of the tribe (Bentham & Hooker, 1873) that included, sometimes with reservations, taxa that we now know were misplaced: the cichorioid Liabeae and *Gongrothamnus* (= *Distephanus*, Vernoniaeae) and the asteroid paleaceous Heliantheae (*Dimeresia*, *Neurolaena*, and *Schistocarpa*), the epaleaceous Heliantheae (*Arnica*, *Malotopus*, *Peucephyllum*, *Psathyrotes*), and the Inulean *Adenocaulon*. For dispositions of these genera, see the studies of the Liabeae (Robinson, 1983), *Distephanus* (Robinson & Kahn, 1986), and the Heliantheae (Robinson, 1981). Ornduff et al. (1963) also felt that the Blennospermatinae were not Senecioneae, but the subtribe is included in the present concept.

The first paper on the Senecioneae in the present series (Ornduff et al., 1963) had many records and comments on the genera that remain in the tribe. Included were a brief mention of *Crocidium* (of the Blennospermatinae) with $n = 9$, some *Emilia* with $n = 5$, examples of species of *Senecio* in Australia

¹ We thank N. S. Lander, P. S. Short, and P. G. Wilson for identification of the Australian members of the tribe. The fieldwork of R. M. King in Ecuador was supported by a National Geographic Society grant. Paul Peterson is thanked by R. M. King for help in collecting in Mexico and Ecuador. Frank Almeda, George Proctor, and Robert Garvey are thanked for help in numerous other field trips. Liz Zimmer is thanked for obtaining reference material. Robert Kowal and B. L. Turner are thanked for careful reviews of the manuscript.

² Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.

³ Department of Botany, University of Hawaii at Manoa, Honolulu, Hawaii 96822, U.S.A.

⁴ Department of Biology, Sul Ross State University, Alpine, Texas 79832, U.S.A.

Table 1. Results. The following are newly reported chromosome counts and citations of vouchers for species of Senecioneae. Species not previously reported are marked with an asterisk (*). K numbers represent King collection numbers. Counts are reported as 2*n* (Carr) or *n* (Powell). Vouchers are in US (duplicates in MO).

Species	Chromosome number	Voucher
* <i>Arnoglossum ovatum</i> (Walt.) H. Rob.	2 <i>n</i> = ca. 28–30 pairs	U.S.A. Florida: Liberty Co., K10297
<i>Barkleyanthus salicifolius</i> (HBK) H. Rob. & Brettell	<i>n</i> = ca. 30	Guatemala. Quezaltenango: K7261
<i>B. salicifolius</i>	<i>n</i> = 30	Guatemala. Totonicapán: K7292
<i>Crassocephalum crepidioides</i> (Benth.) S. Moore	2 <i>n</i> = 20 pairs	Puerto Rico. Mpio. Bayamón, K10607
<i>Emilia coccinea</i> (Sims) Sweet	<i>n</i> = 8 or 9	Dominica. St. Patrick, K6366
<i>E. fosbergii</i> Nicolson	2 <i>n</i> = 10 pairs	Costa Rica. San José: K10023
<i>E. fosbergii</i>	<i>n</i> = ca. 10	Ecuador. Guayas: K6947
<i>E. fosbergii</i>	2 <i>n</i> = 10 pairs	Puerto Rico. Mpio. Salinas, K10598
<i>Erechtites hieraciifolia</i> (L.) Raf. ex DC.	2 <i>n</i> = 20 pairs	U.S.A. Virginia: Fairfax Co., K10596
<i>Erechtites valerianiaeifolia</i> (Wolf) DC.	<i>n</i> = 17–20	Dominica. St. George, K6302
* <i>Gynoxys acostae</i> Cuatrec.	2 <i>n</i> = ca. 40 pairs	Ecuador. Pichincha: K10056
* <i>G. buxifolia</i> (HBK) Cass.	<i>n</i> = ca. 40	Ecuador. Chimborazo: K6602
* <i>G. fuliginosa</i> (HBK) Cass.	2 <i>n</i> = 40 pairs	Ecuador. Carchi: 10117
* <i>G. hallii</i> Hieron.	very sticky, possibly <i>n</i> = ca. 40	Ecuador. Pichincha: K6735
* <i>G. sancti-antonii</i> Cuatrec. var. <i>brevifolia</i> (Hieron.) Cuatrec.	<i>n</i> = 40 + 4–5 B chromosomes	Ecuador. Azuay: K6902
<i>Gynura pseudochina</i> (L.) DC.	<i>n</i> = 10	Thailand. Kamphaeng Phet, K5438
* <i>Jessia cooperi</i> (Greenm.) H. Rob. & Cuatrec.	<i>n</i> = ca. 50	Costa Rica. San José: K6743
* <i>J. cooperi</i>	<i>n</i> = ca. 50	Costa Rica. Cartago: K6771
* <i>J. cooperi</i>	2 <i>n</i> = ca. 49 pairs	Costa Rica. San José: 10031
* <i>Lasiocephalus involucratus</i> (HBK) Cuatrec.	2 <i>n</i> = 20 pairs	Ecuador. Carchi: K10098
* <i>L. involucratus</i>	2 <i>n</i> = 20 pairs	Ecuador. Chimborazo: K10174
* <i>L. patens</i> (HBK) Cuatrec.	2 <i>n</i> = 20 pairs	Ecuador. Carchi: K10083
<i>Pentacalia andicola</i> (Turcz.) Cuatrec.	2 <i>n</i> = 20 pairs	Ecuador. Carchi: K10099
<i>P. andicola</i> var. <i>pseudonitidus</i> Cuatrec.	<i>n</i> = 20	Ecuador. Azuay: K6643
* <i>P. firmipes</i> Greenm.	2 <i>n</i> = 20 pairs	Costa Rica. Cartago: K10022
* <i>P. phanerandra</i> (Cufod.) H. Rob. & Cuatrec.	<i>n</i> = 17 or 20	Costa Rica. Cartago: K6436
<i>P. reflexa</i> (HBK) Cuatrec.	2 <i>n</i> = ca. 50 pairs	Venezuela. Mérida: K10496
<i>P. reflexa</i>	2 <i>n</i> = ca. 50 pairs	Venezuela. Mérida: K10590
* <i>P. sotarensis</i> (Hieron.) Cuatrec.	2 <i>n</i> = ca. 50 pairs	Ecuador. Carchi: K10078
<i>P. vaccinioides</i> (HBK) Cuatrec.	<i>n</i> = 20	Ecuador. Azuay: K6662
<i>P. vaccinioides</i>	2 <i>n</i> = ca. 20 pairs	Ecuador. Carchi: K10088
<i>Psacalium sinuatum</i> (Cerv.) H. Rob. & Brettell	2 <i>n</i> = ca. 30 pairs	Mexico. Durango: K9916
* <i>Pseudogynoxys sonchoides</i> (HBK) Cuatrec.	<i>n</i> = ca. 46	Ecuador. Azuay: K6688
<i>Roldana petasioides</i> (Greenm.) H. Rob. & Brettell	<i>n</i> = 30	Guatemala. Sololá: K7228
<i>R. petasioides</i>	<i>n</i> = ca. 30	Guatemala. Quiché: K7286
* <i>Senecio canchahuinganquensis</i> Cabrera	2 <i>n</i> = ca. 20 pairs	Argentina. Neuquén: K9408
<i>S. costaricensis</i> R. M. King	<i>n</i> = 20	Costa Rica. Cartago: K5392, Type
<i>S. costaricensis</i>	<i>n</i> = ca. 17	Costa Rica. San José: K6759
<i>S. coahuilensis</i> Greenm.	2 <i>n</i> = 23 pairs	Mexico. Coahuila: K10356
<i>S. culcitoides</i> Wedd.	2 <i>n</i> = 20 pairs	Ecuador. Pichincha: K10051
<i>S. deferens</i> Griseb.	2 <i>n</i> = 20 pairs	Argentina. Catamarca: K9465
<i>S. douglasii</i> DC.	2 <i>n</i> = 20 pairs	Mexico. Sonora: K9806
<i>S. elegans</i> L.	2 <i>n</i> = ca. 10 pairs	Australia. Victoria: K10268
<i>S. flavus</i> (Decne.) Sch. Bip.	2 <i>n</i> = 10 pairs	Morocco. Quarzazate: K10653
<i>S. glomeratus</i> Desf. ex Poir.	2 <i>n</i> = 30 pairs	Australia. Victoria: K9705
<i>S. gunnii</i> (Hook. f.) Belcher	2 <i>n</i> = 20 pairs	Australia. Victoria: K9767
<i>S. gunnii</i>	2 <i>n</i> = 20 pairs	Australia. Victoria: K9773

Table 1. Continued.

Species	Chromosome number	Voucher
* <i>S. hieronymi</i> Griseb.	2 <i>n</i> = 10 pairs	Argentina. Buenos Aires: K10289
<i>S. jacobaea</i> L.	2 <i>n</i> = 20 pairs	Australia. Victoria: K9785
<i>S. lautus</i> G. Forst. ex Willd.	2 <i>n</i> = ca. 20 pairs	Australia. Western Australia: K9531
<i>S. lautus</i>	2 <i>n</i> = 10 pairs	Australia. Western Australia: K9597
<i>S. lautus</i>	2 <i>n</i> = 20 pairs	Australia. Victoria: K9776
<i>S. lautus</i>	2 <i>n</i> = ca. 20 pairs	New Zealand. North Island: K10266
<i>S. linearifolius</i> A. Rich.	2 <i>n</i> = 30 pairs	Australia. Victoria: K9739
<i>S. linearifolius</i>	2 <i>n</i> = 30 pairs	Australia. Victoria: K9752
<i>S. linearifolius</i>	2 <i>n</i> = ca. 30 pairs	Australia. Victoria: K9786
<i>S. linearifolius</i>	2 <i>n</i> = ca. 30 pairs	Australia. New South Wales: K9975
<i>S. lucidus</i> (Sw.) DC.	<i>n</i> = ca. 50	Dominica. St. George: K6379
<i>S. lucidus</i>	2 <i>n</i> = 50–52 pairs	France. Martinique: K10647
<i>S. madagascariensis</i> Poir.	2 <i>n</i> = 10 pairs	Australia. New South Wales: K9972
<i>S. minimus</i> Poir.	2 <i>n</i> = 30 pairs	Australia. Victoria: K9741
<i>S. nivalis</i> (HBK) Cuatrec.	2 <i>n</i> = 20 pairs	Ecuador. Pichincha: K10045
<i>S. odoratum</i> Hornem.	2 <i>n</i> = 30 pairs	Australia. Victoria: K9754
<i>S. pterophorus</i> DC.	2 <i>n</i> = 10 pairs	South Africa. Natal: K10205
<i>S. pterophorus</i>	2 <i>n</i> = 10 pairs	South Africa. Cape: K10215
<i>S. purpureus</i> L.	2 <i>n</i> = 10 pairs	South Africa. Cape: K10212
<i>S. aff. purpureus</i>	2 <i>n</i> = 10 pairs	South Africa. Natal: K10207
* <i>S. rigidus</i> L.	2 <i>n</i> = 10 pairs	South Africa. Cape: K10220
<i>S. runcinatus</i> Less.	<i>n</i> = 17 or 20	Mexico. Veracruz: K6497
<i>S. rudbeckiaefolius</i> Meyen & Walp.	2 <i>n</i> = 20 pairs	Bolivia. Cochabamba: K9639
* <i>S. subulatus</i> G. Don ex Hook & Arn.	2 <i>n</i> = 20 pairs	Argentina. Río Negro: K9349
* <i>S. subumbellatus</i> Phil.	2 <i>n</i> = ca. 20 pairs	Argentina. Mendoza: K9423
* <i>S. tephrosioides</i> Turcz.	2 <i>n</i> = 20 pairs	Ecuador. Sucumbíos: K10126
<i>S. vagans</i> F. Muell.	2 <i>n</i> = ca. 49 pairs	Australia. Victoria: K9750
<i>S. veilleiodes</i> A. Cunn. ex DC.	2 <i>n</i> = ca. 19 pairs	Australia. Victoria: K9748
<i>S. veilleiodes</i>	2 <i>n</i> = 19 pairs	Australia. Victoria: K9788
<i>S. viravira</i> Hieron.	2 <i>n</i> = 20 pairs	Argentina. Río Negro: K9360
<i>S. viravira</i>	2 <i>n</i> = 20 pairs	Argentina. La Rioja: K9457
<i>S. warszewiczii</i> A. Br. & Bouché	<i>n</i> = 20	Guatemala. Chimaltenango: K7200
<i>S. warszewiczii</i>	<i>n</i> = 20	Guatemala. Quezaltenango: K7029

and the genus *Ligularia* and its relatives with *n* = 30, and a discussion of the *Senecio aureus* group with *n* = 22–24. The paper ends with, “The occurrence of species of *Senecio* with *n* = 10 in portions of Europe and Africa, and the concentration of Senecioninae and Othonninae with *n* = 10 in Africa strongly suggest an Old World origin for the tribe, with subsequent wide migration and diversification nearly throughout the world.” These points are enlarged upon below. The present paper adds and discusses a few chromosome records of note from the Andean genera that were previously reported cytologically only by Turner et al. (1967) and Powell and Cuatrecasas (1970).

Within the Senecioneae, at the subtribal and generic levels, two particular microcharacters have come into taxonomic use: (1) the anther collar being

cylindrical versus balusterform (with a zone of enlarged cells below, Robinson & Brettell, 1973b; Nordenstam, 1978; Vincent, 1996), and (2) the stigmatic surface covering the whole inside of the style branch versus forming two separated lines on each branch. These characters were observed and illustrated by Cassini (1818), but they were cited only sparingly afterwards until they were used to delimit the generic concepts of *Senecio* sensu lato and the Tussilaginae (as cacalioids) by Robinson and Brettell (1973b) and Nordenstam (1978). This narrower concept of *Senecio* has been resisted by some authors, and the value of the microcharacters has been questioned due to some variability (Wetter, 1983); however, the value of the microcharacters is now generally recognized (Vincent, 1996) and the narrower generic concepts are now generally ac-

cepted (Jeffrey, 1992; Nordenstam, 1996b; Barkley et al., 1996; Vision & Dillon, 1996).

MATERIALS AND METHODS

The new reports in this paper are based on material collected by R. M. King and counted by G. D. Carr (reported as $2n$) and A. M. Powell (reported as n). The chromosome counts have been made from aceto-carmin or aceto-orcin squashes of microsporocytes in meiosis. Voucher specimens are in US and a second set is at MO.

DISCUSSION

Blennospermatinae, $x = 9$

Ornduff et al. (1963) strongly suggested that *Crocidium* did not belong to the Senecioneae. However, the TEM study of pollen (Skvarla & Turner, 1966) and flavonoid data (Ornduff et al., 1973) support placement of both *Crocidium* and *Blennosperma* in the tribe. Inclusion of *Crocidium* in the Senecioneae, in a subtribe Crocidiinae (= Blennospermatinae), was accepted by Robinson and Brettell (1973a), with the addition of *Ischnea*. The latter addition was supported by the TEM study by Gadek et al. (1989). The subtribe is distinguished within the tribe by small pollen, 23–25 μm diam., measured in fluid, as in the Astereae. Cytologically, *Blennosperma* has $n = 7, 9$; *Crocidium* $n = 9$ (Jeffrey, 1992), and *Ischnea* $n = 9$ (Borgmann, 1964). The subtribe is evidently a basal offshoot of the Senecioneae with an aneuploid reduction series of chromosome numbers from $x = 10$.

Abrotanellinae H. Rob., G. D. Carr, R. M. King & A. M. Powell, subtribus nov., $x = 9$. TYPE: *Abrotanella* Cass.

Plantae herbaceae perennes caespitosae ad 12 cm altae; folia rosulata, laminis glandulo-punctatis; capitula disciformia; flores peripherales feminei, ramis stylium brevibus, stigmatibus marginalibus; flores interiores masculini vel hermaphroditi; corollae pallidae, tubis interne ad apicem non annulate ornatis, filamenta in partibus superioribus cylindracea; rami stylium breves vel nulli, stigmatibus marginalibus vel nullis; achaenia glabra vel raro setulifera; grana pollinis 27–40 μm diam.; chromosomatum numerus $2n = 18, 36$.

Abrotanella of South America and the Australasian species that have been placed in that genus were included in the Blennospermatinae by Nordenstam (1977), Bremer (1994), and Swenson (1995a, b), but are excluded from the subtribe here. The base chromosome number of $x = 9$ seems to isolate the group from all members of the Senecioneae except the Blennospermatinae, and *Abrota-*

nella has glandular-punctate leaves, disciform heads, more incrassate corolla tissue, and no annulus inside at the base of the corolla limb (Robinson & Brettell, 1973a), all of which distinguish it from the Blennospermatinae. The hairs of the achenes, when present, are never the mucilage hairs seen in members of all three genera of the Blennospermatinae. The somewhat larger pollen grains and the texture of the corollas in the Abrotanellinae are more like other Senecioneae than like the Blennospermatinae. The habit of *Abrotanella* is similar to that of *Werneria* and *Xenophyllum*, but the latter clearly belong to the Senecioninae with balusterform anther collars and chromosome numbers of $n = \text{ca. } 50$ or higher in most species.

Tussilaginae, $x = 30$

One group mentioned by Jeffrey (1992) with $n = 30$, the tussilaginoid group or Tussilagininae, contains many mostly Northern Hemisphere genera, some of which were included within *Senecio* in the traditional classification of the tribe (Bentham & Hooker, 1873). The group is characterized by cylindrical anther collars, stigmatic papillae continuous over the inner surface of the style branches, and a strong tendency for palmately veined or peltate leaves. Included are many species outside of Europe that were placed in *Cacalia*, but excluded is *Hasteola* (Anderson, 1994). Sixteen species from various genera with counts of $n = 25, 26, 28, 29$, and 30 were reported by Ornduff et al. (1963, 1967). Counts of $n = 30$ were reported for 15 eradiate, white-flowered Mexican species of the group by Pippen (1968). Counts for a few more Mexican members of the group were reported by Powell et al. (1974). Robinson and Brettell (1974) first generally recognized the Tussilagininae (as the caca-lioid group) and correlated it with the chromosome number of $n = 30$, listing the 27 Mexican species then known to have this number. The correlation was also noted by Nordenstam (1977). The Central American genera were reviewed by Barkley et al. (1996) with some recent additions such as *Robinsonecio*, with $n = 30$ (Barkley & Janovec, 1996). The summary of the 35 European, Asiatic, Australian, North American, and Mexican genera of the group by Jeffrey (1992) shows $n = 30$ as the primary or only chromosome number in 25 of the 30 genera that have been sampled cytologically. Some genera have variations from $n = 30$ (Jeffrey, 1992), especially aneuploid reductions: to $n = 25$ or ca. 25 in *Arnoglossum* and *Psacalium*; to $n = 26$ in *Parasenecio*, *Miricacalia*, and *Syneilesis*; and to n

= 28 in *Rugelia* and *Endocellion*. Lower numbers occur in some genera, within which $n = 30$ predominates: $n = 16$ and 24 in *Ligularia*, $n = 15$ and 20 in *Doronicum*, and $n = 14$ and 16 in *Petasites*.

Although a simple point, it should be noted that $n = 30$ in the Senecioneae is not a simple polyploid derivative of $n = 10$ like $n = 20$, 40, or 80, but requires two steps: first a tetraploid ($n = 20$) crossing with a diploid ($n = 10$) to give a triploid ($2n = 30$), which then is stabilized by a second doubling to $2n = 60$ giving $n = 30$. In the Tussilagininae with lower chromosome numbers, only *Doronicum* has $n = 15$ and 20. *Ligularia* has $n = 16$, with the next lowest number at 24, and *Petasites* has $n = 14$ and 15, with the next lowest number at 26. These lower numbers in the group, of mostly European origin, cannot be ancestral if $n = 30$ is basic to the Tussilagininae. At present, these lower numbers are considered extreme reductions, far exceeding the modest aneuploid reductions seen in other members of the group such as *Arnoglossum*, *Rugelia*, and the Asiatic genera *Parasenecio*, *Miricacalia*, and *Syneilesis*.

While $n = 30$ seems to be basic in the Tussilagininae, that number also occurs in some members of the Senecioninae, mentioned below. Also, the aneuploid reductions in the Tussilagininae approach or duplicate the aneuploid increases in the Senecioninae, e.g., the aureoid group with $n = 22$, 23.

Gynoxoid group, $n = 40$

Jeffrey (1992) listed a few, mostly American, genera as gynoxoid, including *Gynoxys*, *Paragynoxys*, *Paracalia*, and *Aequatorium*. For information on the most recent additions to *Gynoxys*, *Aequatorium*, and *Paragynoxys*, see Robinson and Cuatrecasas (1992). These genera have a single continuous stigmatic surface on the inside of the style branches and cylindrical anther collars like the Tussilagininae, and *Gynoxys* falls generally with the tussilaginoid genera in the cpDNA study of Kadereit and Jeffrey (1996). The one feature that might hold the group apart from the Tussilagininae is the chromosome number of $n = 40$ or ca. 40 in *Paragynoxys* ($n = 38$ –40 pairs, Powell & Cuatrecasas, 1970) and *Gynoxys* (Turner et al., 1967; this paper). Counts for two species of *Gynoxys* have been reported previously: *G. hutchisonii* H. Rob. & Cuatrec. (as *G. parvifolia* Cuatrec.) and *G. tomentosissima* Cuatrec. (Turner et al., 1967), with $n =$ ca. 40 or $40 + B$'s. Counts for five additional Ecuadorian species are reported in the present study, all

with $n = 40$ or ca. 40, one of these with 4–5 B chromosomes.

The dioecious genus *Chersodoma* (Dillon & Sagástegui-Alva, 1996) of southern South America has $2n = 20$ (Hunziker et al., 1989) based on one species, *C. argentina* Cabrera, and was placed in the Senecioninae near *Senecio* by Jeffrey (1992). However, the anther collars are cylindrical and the stigmatic surfaces cover the inside of at least the distal halves of the style branches (Robinson & Brettell, 1973b), for which reasons we provisionally place the genus near the Tussilagininae.

Senecioninae

(1) Some elements with $n = 30$ and $n = 50$

The chromosome number $n = 30$ is inevitable in any large group that has a base of $x = 10$ and many multiples of that number. Of special interest are groups in the Senecioneae that have stabilized at $n = 30$. Jeffrey (1992) mentioned a number of such groups. One in which $n = 30$ seems to be basic is the Tussilagininae. Others appear to be derived separately within the Senecioninae (Jeffrey, 1992), such as *Pericallis* and a group of Australian *Senecio* that was sampled by Ornduff et al. (1963) and studied extensively by Lawrence (1980, 1985a, b).

In the Macaronesian *Pericallis* with 15 species, including the common "Cineraria" of horticulture, $n = 30$ occurs in all eight species that have been counted (Jeffrey, 1992).

A group of Australian species of *Senecio* with $n = 30$ includes one radiate species, five discoid, and four classified as erectitoid (Lawrence, 1980). Six of the Australian species of *Senecio* with $n = 30$ are self-incompatible perennial herbs, and six others, including *S. biserratus* Belcher, which have $n = 50$, are self-compatible annuals (Lawrence, 1985a, b). Unlike the Tussilagininae with $n = 30$, this group of unusually abundant Australian hexaploids was considered morphologically typical of the genus *Senecio* Lawrence (1985a). Lawrence further suggested that strict autoploidy in the Australian species was unlikely since no known native diploids appeared to exist. However, both diploid and tetraploid counts are reported here for the common Australian species *S. lautus*. As this is the first report of $n = 10$ for an Australian *Senecio*, additional populations of *S. lautus* should be surveyed in order to determine the frequency and extent of this chromosome condition. Regular meiosis without multivalents was observed in the Lawrence study, even in the highest, decaploid, levels.

In the Senecioneae, $n = 50$ has an origin analogous to that of $n = 30$: a cross of $n = 20$ with n

= 30 and a doubling to give $2n = 100$. The number is apparently basic to the Costa Rican/Panamanian species of *Jessea* (Robinson & Cuatrecasas, 1994; Nordenstam, 1996a), included in *Jacmaia* by Jeffrey (1992). Two species were known to have $n =$ ca. 50 (Jeffrey, 1992), and our three counts of *J. cooperi* are the same.

The African *Dendrosenecio* is reported to have chromosome numbers of $n = 10$, ca. 40, and 50 (Jeffrey, 1992); however, Knox and Palmer (1995) and Knox (1996) accepted the conclusions of Knox and Kowal (1993) that the genus consistently has $n = 50$ and the other numbers are in error. Knox and Palmer (1995) stated, "The giant senecios, apparently decaploid ($n = 50$), show virtually no meiotic irregularities that might suggest a recent origin from the predominantly tetraploid ($n = 20$) putatively close relatives suggested in the literature." Knox and Kowal (1993) mentioned many comparatively unrelated elements of the Senecioneae that share the number $n = 50$, including the Australian *Arrhenechthites*, African *Kleinia*, neotropical *Dendrophorbium*, *Graphistylis*, *Jessea* (as *Jacmaia*), *Pentacalia*, and *Xenophyllum* (as *Werneria*). Study of cpDNA indicated that the closest relatives of *Dendrosenecio* are the African genera *Cineraria* ($n = 10$) and *Euryops* (mostly $n = 10$, seldom $n = 20, 30$) (Knox & Palmer, 1995; Knox, 1996). A separate cpDNA study (Kadereit & Jeffrey, 1996) placed *Dendrosenecio* as the most divergent member of a diverse group including the neotropical *Pseudogynoxys* and *Dorobaea* and the Macaronesian *Pericallis*, but unfortunately neither *Cineraria* nor *Euryops* were included in the study.

(2) The aureoid senecios, $n = 22, 23$

The aureoid senecios, often treated as a separate genus, *Packera*, have the appearance and almost all the technical characteristics of *Senecio* sensu stricto. The aureoid species have been treated in *Senecio* as subgroups *Aurei*, *Bolanderiani*, *Lobati*, *Sanguisorboidei*, and *Tomentosi* in Ornduff et al. (1963, 1967), with reports of $n = 22, 23$, or 24 from 22 species. Additional records were provided by Kowal (1975) and Bain (1985), and the group was discussed by Barkley (1988), who stated that chromosome numbers had been reported for 48 of the 59 species. Our count of $n = 23$ for the Mexican *Senecio coahuilensis* agrees with previous reports for the species and is the commonest number in the group. Some 15 or 16 species occur in Mexico (Freeman & Barkley, 1995; Barkley et al., 1996). Counts of $n = 20$ for *Senecio flettii* Wiegand and *S. bellidifolius* HBK are anomalous in the aureoid group (Barkley, 1988), but *S. bellidifolius* is well nested within the aureoid group on the basis

of ITS sequence data and pollen structure (Bain & Jansen, 1995). Kowal (1994) cited ca. 65 species in the group, all in North America from Mexico to the Arctic, with one Arctic-alpine species extending into Asia. Most species have $n = 23$, and $n = 22$ occurred only in seven species in the area of most diversity, including four species restricted to eastern North America (Kowal, 1994). Counts of $n = 20$ and 40 in *Senecio pseud aureus* were probably wrong (Kowal, 1994).

Packera, with *Senecio aureus* L. as type, was accepted as a genus by Jeffrey (1992) using such structural characters as lack of interfascicular cambium, branching fibrous roots, apparently obscure carpodia, and specific forms of apically flagellate hairs, which are neither exclusive to the aureoid group nor very convincing. The group lacks the fluked pappus of typical *Senecio* (Drury & Watson, 1966), but so do many other elements of *Senecio*. A more substantial difference is the helianthoid ultrastructure of the pollen wall (exine with internal foramina), which occurred in all 19 aureoid species examined in sections *Aurei*, *Tomentosi*, and *Lobati* (Bain & Walker, 1995), and the latter authors questioned the value of continuing to recognize the sections. Non-aureoid North American species examined, including some tephroseroid Senecioneae (*Tephroseris*, *Tussilagininae*, $x = 24$) and the *Senecio* sections *Lugentes*, *Integerrimi* ($n = 20$), and *Triangulares* ($n = 10, 18, 20, 40$), had a senecioid exine wall pattern (lacking internal foramina).

A few features of the aureoid senecios are clear. It is the only significant element of the Senecioneae in which the chromosome number does not readily fit the general pattern derived from $x = 10$ and its multiples, although it may have been derived by an aneuploid increase from groups with $n = 20$, to which it seems otherwise closely related. The number $n = 20$ has been reported in the group (Barkley, 1988), but Kowal (1994) considered this an error. Also, the number $n =$ ca. 30 has been reported for *S. sanguisorbae* DC. (Turner et al., 1961), for which all other counts are $n = 23$. Chromosome numbers of this group might be more unstable than in taxa with $x = 10, 20, 30$, or 50.

Unfortunately, the best characters differentiating the aureoid senecios have limited value for ordinary taxonomic identification. Neither chromosome number nor ultrastructure of the pollen exine is readily observable. The lineage is distinct, but the phyletic distance from typical *Senecio* may still be comparatively slight. *Senecio aureus* falls into a group of intermixed *Senecio-Kleinia-Gynura* species in the cpDNA study of Knox and Palmer (1995). The evidence could be used to justify many further seg-

regates from *Senecio*, but the necessary detailed studies are still to be done. Recognition of *Packera* as a distinct genus seems premature at this time.

(3) *Mulgedifolii* group, $n = 20, 40$

The *Mulgedifolii* group of Mexico lacks ray florets and has red or white, but never yellow, corollas. The combination of characters led some early authors to place some of the species in the broad concept of *Cacalia*, and they appear among the excluded taxa listed by Pippen (1968). The *Mulgedifolii* have the characteristic balusterform anther collars and separate stigmatic lines of the Senecioninae. The group was retained in *Senecio* by Barkley et al. (1996). There is a report of $n = 22$ for *S. runcinatus* Less. (Keil & Stuessy, 1975), and the same species is reported here as $n = 17$ or 20. Kowal (pers. comm.) has indicated that the $n = 22$ was probably wrong. The unpublished summaries of the *Mulgedifolii* chromosome counts by Villaseñor list 10 counts for 6 species (1986) and 33 counts for 15 of the 17 species (1991). All listed counts, except the dubious $n = 22$, are $n = 20$ with one tetraploid $n = 40$.

(4) *Emilia*, $n = 5$

Emilia continues to show chromosome numbers of $n = 5$ and 10 (Baldwin, 1946). The related African species of *Senecio* that were reported with $n = 5$ by Turner and Lewis (1965) and Lawrence (1985a, b) have all been transferred to *Emilia* by Jeffrey (1986). The lower numbers correlate with the short-lived, weedy habit of the genus. This situation parallels that of *Fleischmannia microstemon* (Cass.) K. M. King & H. Rob. (Baker, 1967) and many other short-lived species with lower DNA content (Bennett, 1972). The low number is considered here a derived condition in *Emilia*, a reorganization of chromatin on fewer centromeres as in *Fleischmannia microstemon* (Baker, 1967) and *Crepis* (Tobgy, 1943). Such a reorganization, or "genome congealing" (Wagner et al., 1993: 422–423) has been supported by a measurement of the nuclear DNA content of *E. discifolia* (Oliv.) C. Jeffrey (as *Senecio discifolius* Oliv.) (Lawrence, 1985b).

In structural features, *Emilia* is a member of the Senecioninae, with paired stigmatic lines and balusterform anther collars, and comes out in the general subgroup with *Othonna* and *Dendrosenecio* in the cpDNA study of Kadereit and Jeffrey (1996).

(5) Senecioninae with $n = 10, 20$

In the Senecioneae, $n = 10$ is largely restricted to Europe and Africa in the Eastern Hemisphere (Ornduff et al., 1963), and the pattern is reinforced by new reports in the present study. A few interesting exceptions occur. *Emilia*, with $n = 5$ and 10, is only a recent introduction into the New World

from the Old World. The one old citation of $n = 10$ in the neotropical *Pseudogynoxys*, questioned by Jeffrey (1992), must be incorrect. All other reports for the genus are $n = 45–48$ including *P. chenopodioides* (HBK) Cabrera with $n = 45 + 5$ (Turner et al., 1962, as *S. confusus* Britton) and our report of *P. sonchoides* (HBK) Cuatrec., representing two morphological extremes of the genus. Jeffrey's (1992) summary also gives both $n = 10$ and $n = 20$ for *S. flaccidus* Less. of Mexico and *S. brasiliensis* (Spreng.) Less. of South America. These isolated occurrences of $n = 10$ in basically $n = 20$ groups seem unlikely to be survivors of an ancestral number, but are more likely reductions resulting from polyploidy or aneuploid reduction as in *Emilia* and some Tussilaginatae such as *Doronicum*, *Ligularia*, and *Petasites*.

An interesting close relationship between an African species with $n = 10$ and an American species with $n = 20$, both autogamous, annual, desert species, is suggested by isozyme analysis (Liston et al., 1989) and cpDNA evidence (Liston & Kadereit, 1995). In these papers, the North American *Senecio mohavensis* A. Gray was considered a closely related derivative, through long-distance dispersal, of *S. flavus* (Decne.) Sch. Bip. subsp. *breviflorus* Kadereit of the Saharo-Arabian deserts.

Radford et al. (1995) indicated that the aggressively weedy taxon commonly identified as *Senecio madagascariensis* Poir. was consistently $2n = 20$ based on material from Madagascar, South Africa, Australia, and Argentina specimens, and our count is the same. In contrast, Radford et al. (1995) reported the common Australian species *S. lautus* G. Forst. ex Willd. as consistently $2n = 40$ (see also the present study; Turner, 1970; Lawrence, 1980; Webb, 1988). However, see the report here of $2n = 10$ pairs for material determined by Lander, Short, and Wilson as *S. lautus* from Western Australia. Sindel (1996) summarized the literature on the four subspecies of *S. lautus*.

(6) Andean genera *Lasiocephalus* and *Pentacalia*, $n = 20, 30, 45–52$

Our counts confirm the few previous counts for two Andean genera. Further work on chromosome numbers of Andean Senecioneae is needed. *Lasiocephalus* (including *Aetheolaena*) has previously been known cytologically from one species, *L. loeseneri* (Hieron.) Cuatrec. (Turner et al., 1967). Counts for additional species, *L. involucratus* (HBK) Cuatrec. and *L. patens* (HBK) Cuatrec., are reported in the present study. All three species show $n = 20$.

Robinson and Cuatrecasas (1978) resurrected *Pentacalia* from synonymy within *Senecio* and in-

cluded 13 Central American species. Cuatrecasas (1981) transferred 177 South American species into *Pentacalia*. He accepted two subgenera, the often scandent subgenus *Pentacalia* and the often heath-like subgenus *Microchaete*. Jeffrey (1992) split *Pentacalia* into three groups: typical *Pentacalia*; a new genus *Monticalia* Jeffrey, roughly equivalent to the subgenus *Microchaete*; and a broadly delimited genus *Dendrophorbium*. The broader view of *Pentacalia* is retained here because of some unresolved problems of intergradation. In personal discussion, Cuatrecasas pointed out that, while most members of subgenus *Pentacalia* are scandent, the type species, *P. arborea* (HBK) H. Rob. & Cuatrec., and its closest relatives are trees with hanging branches. The isolated branches can be mistaken for vines. Thus, the nature of the type species complicates any tendency to base generic distinctions on habit. The genus *Monticalia* is not considered distinct from *Pentacalia* here. In any case, priority would go to *Scrobicaria*, which was imperfectly distinguished from *Monticalia* only by its opposite leaves and which was recently reduced to synonymy under *Pentacalia* (Cuatrecasas, 1994). *Dendrophorbium* is also interpreted more narrowly here to include only its more typical element that usually lacks tails on the bases of the anthers. As a result, the following chromosome counts cited by Jeffrey (1992) all fall within *Pentacalia* sensu lato: *Pentacalia* $n = 20$ (1 sp.), ca. 40 (1 sp.), 45–50 (2 spp.), 50 (1 sp.), and ca. 51 (1 sp.); *Dendrophorbium* $n =$ ca. 40, 49–50 based on 1 sp.; and *Monticalia* $n = 20$ (9 spp.) and $40 + 1-5$ (1 sp.). The reports in the present study, of which three are new, show the same range of numbers, $n = 20$, $n = 17$ or 20, and $n =$ ca. 50. The higher numbers in *Pentacalia* have undoubtedly arisen many separate times in higher elevation members of the genus.

Senecio lucidus (Sw.) DC., from the Lesser Antilles, is reported here with $n =$ ca. 50 and $2n = 50-52$ pairs. The species evidently belongs to *Pentacalia*, but dispositions of West Indian species of the group are very incomplete (Robinson, 1982).

(7) *Culcitium* and *Dorobaea*, $n = 20, 50$

Culcitium sensu stricto ($n = 20$) and *Dorobaea* ($n =$ ca. 50), from the northern Andes, have fistulose receptacles and a rosulate habit with decrescent or progressively smaller upper leaves. For these reasons, Jeffrey (1992) and others, including Robinson, have considered both genera as part of *Senecio*, in spite of their individually distinctive appearances. Recent cpDNA evidence placed *Dorobaea* in a lineage with *Dendrosenecio* and *Pseudogynoxys*, less close to *Emilia* and *Othonna*, and isolated from *Senecio* sensu stricto (Kadereit & Jef-

frey, 1996). Both Andean genera have stigmatic lines and anther collars of the Senecioninae. On the basis of the cpDNA study, *Dorobaea* (3 sp., Nordenstam & Pruski, 1995) and the probably closely related *Culcitium* sensu stricto are recognized here as distinct genera.

(8) *Werneria* and segregates, $n =$ ca. 50, 100

Werneria has been treated very broadly in the past to include many densely leaved, rosulate or strobiform species in tropical America specialized for high elevations. Genera recently segregated by Funk (1997a, b, c) are *Xenophyllum*, including two species with $2n =$ ca. 104 ± 4 and $2n =$ ca. 108 ± 4 (Diers, 1961), and the monospecific *Misbrookea*, with $n =$ ca. 106 ± 4 (Diers, 1961). The type of *Werneria*, *W. nubigena* HBK, has been reported as $2n =$ ca. 212 ± 8 from Peru (Diers, 1961) and as $n = 50$ from Guatemala (Beaman & Turner, 1962). Other Andean species that presently remain in *Werneria*, for which Diers's (1961) counts are available, include *W. apiculata* Sch. Bip. with $2n =$ ca. 206 ± 8 , *W. orbignyana* Wedd. with $2n =$ ca. 100 ± 4 , *W. caespitosa* Wedd. with $2n =$ ca. 154 ± 6 , *W. pygmaea* Gillies ex Hook. & Arn. with $2n =$ ca. 212 ± 8 , *W. solivifolia* Sch. Bip. with $2n =$ ca. 42 ± 2 , *W. spathulata* Wedd. with $2n =$ ca. 106 ± 4 , and *W. villosa* A. Gray with $2n =$ ca. 150 ± 6 . The high chromosome numbers that predominate in the group are evidently associated with the harsh environment of the high-elevation Andes.

Adenostylineae Benth. & Hook. f., $x = 20$

Jeffrey (1992) recognized, within his Senecioninae, a Eurasian group of perennial rhizomatous herbs with 4-lobed corollas. The group includes the genus *Cacalia* ($n = 19$), in its Linnaean sense (Robinson & Brettell, 1973b), which is the same as the later-named *Adenostyles*, and the subtribal name Adenostylineae is applied here. Other genera included in the group are *Dolichorrhiza* ($n = 15-16, 20, 22$), *Iranecio* ($n = 12, 20$), and *Pojarkovia* ($n = 20$) (Jeffrey, 1992). A fifth genus, *Caucasalia* ($n = 19$), has been described by Nordenstam (1997), who has suggested base numbers of $n = 20$ for *Dolichorrhiza*, *Iranecio*, and *Pojarkovia*. The distribution of the numbers suggests more than one aneuploid reduction series from $x = 20$.

CONCLUSIONS

Comparisons between recent taxonomy in the Senecioneae and available chromosome counts have demonstrated again the important point already suggested in the study of the Heliantheae (Robinson et al., 1981): that a phyletic taxonomy can rare-

ly be constructed primarily on the basis of chromosome counts, but chromosome counts usually make sense at some level when compared with a phyletic taxonomy. The positions of the most divergent elements of the tribe, Blennospermatinae and Abrotanellinae, with $x = 9$, could have been foreseen using either taxonomic or cytological approaches. In the remainder of the Senecioneae, significant chromosome number patterns usually recur frequently, such as $x = 30$ in the distinctive Tus-silaginae but also in a number of separate elements of the Senecioninae. Some of the more unique chromosome number trends in the tribe, such as $n = 5$ in *Emilia* and $n = 22, 23$ in the aureoid group of *Senecio*, are taxonomically comparatively close to typical *Senecio*. Some genera such as *Dendrosenecio* of Africa, the Macaronesian *Pericallis*, the tropical American *Jessia* and *Pentacalia*, and an Australian group still placed in *Senecio*, seem to stabilize at counts of $n = 30$ and $n = 50$. Still other members of the tribe, including some related pairs of species in *Senecio*, show simple polyploid variations between $n = 10$ and $n = 20$.

Some taxonomically distinctive groups of the Senecioneae show distinctive chromosome counts. Nevertheless, separate elements of the tribe with the same counts and evidence of different numbers in closely related groups indicate the peril of trying to justify generic or subtribal distinctions in the tribe solely on the basis of chromosome counts.

Literature Cited

- Anderson, L. C. 1994. A revision of *Hasteola* (Asteraceae) in the New World. *Syst. Bot.* 19: 211–219.
- , D. W. Kyhos, T. Mosquin, A. M. Powell & P. H. Raven. 1974. Chromosome numbers in Compositae, IX: *Haplopappus* and other Astereae. *Amer. J. Bot.* 61: 665–671.
- Bain, J. F. 1985. Chromosome numbers in the aureoid *Senecio* complex (Asteraceae). *Canad. J. Bot.* 63: 539–542.
- & R. K. Jansen. 1995. A phylogenetic analysis of the aureoid *Senecio* (Asteraceae) complex based on ITS sequence data. *Pl. Syst. Evol.* 195: 209–219.
- & J. Walker. 1995. A comparison of the pollen wall ultrastructure of aureoid and non-aureoid *Senecio* species (Asteraceae) in North America. *Pl. Syst. Evol.* 195: 199–207.
- Baker, H. G. 1967. The evolution of weedy taxa in the *Eupatorium microstemon* species aggregate. *Taxon* 16: 293–300.
- Baldwin, J. T. 1946. Cytogeography of *Emilia* Cass. in the Americas. *Bull. Torrey Bot. Club* 73: 18–23.
- Barkley, T. M. 1988. Variation among the aureoid *Senecios* of North America: A geohistorical interpretation. *Bot. Rev. (Lancaster)* 54: 82–106.
- & J. P. Janovec. 1996. *Robinsonecio* (Asteraceae: Senecioneae) a new genus from Mexico and Guatemala. *Sida* 17: 77–81.
- , B. L. Clark & A. M. Funston. 1996. The segregate genera of *Senecio sensu lato* and *Cacalia sensu lato* (Asteraceae: Senecioneae) in Mexico and Central America. In D. J. N. Hind & H. J. Beentje (editors), *Compositae: Systematics. Proceedings of the International Compositae Conference*, Kew, 1994. Vol. 1: 613–620. Royal Botanic Gardens, Kew.
- Beaman, J. H. & B. L. Turner. 1962. Chromosome numbers in Mexican and Guatemalan Compositae. *Rhodora* 64: 271–276.
- Bennett, M. D. 1972. Nuclear DNA content and minimum generation time in herbaceous plants. *Proc. Roy. Soc. London, Ser. B, Biol. Sci.* 181: 109–135.
- Bentham, G. & J. D. Hooker. 1873. Compositae. In *Genera plantarum* 2(1): 163–533.
- Borgmann, E. 1964. Anteil der Polyploidien in der Flora des Bismarcksgebirges von Ostneuguinea. *Z. Bot.* 52: 118–172.
- Bremer, Kåre. 1994. *Asteraceae: Cladistics & Classification*. Timber Press, Portland, Oregon.
- Cassini, H. 1818. Composées. In G. Cuvier (editor), *Dictionnaire des Sciences Naturelles* 10: 131–159, 3 pl. Paris. [Reprinted in R. M. King & H. W. Dawson (editors). 1975. *Cassini on Compositae*. Pp. 110–138, pl. 1–3. Oriole Editions, New York.]
- Cuatrecasas, J. 1981. Studies in neotropical Senecioneae II. Transfers to genus *Pentacalia* of north Andean species. *Phytologia* 49: 241–260.
- . 1994. Miscellaneous notes in Neotropical Flora XXII. Identification of the genus *Phyllostelidium* and a few new combinations in the Compositae. *Phytologia* 76: 402–405.
- Diers, L. 1961. Der Anteil an Polyploidien in den Vegetationsgürteln der Westkordillere Perus. *Z. Bot.* 49: 437–488.
- Dillon, M. O. & A. Sagástegui-Alva. 1996. Revision of the dioecious *Chersodoma* Phil. (Senecioneae, Asteraceae), including a new species and status change. *Brittonia* 48: 582–602.
- Drury, D. G. & L. Watson. 1966. A bizarre pappus form in *Senecio*. *Taxon* 15: 309–311.
- Freeman, C. C. & T. M. Barkley. 1995. A synopsis of the genus *Packera* (Asteraceae: Senecioneae) in Mexico. *Sida* 16: 699–709.
- Funk, V. A. 1997a. *Misbrookea*, a new monotypic genus removed from *Werneria* s.l. (Compositae: Senecioneae). *Brittonia* 49: 110–117.
- . 1997b. *Werneria* s.l. (Compositae: Senecioneae) in Ecuador. Pp. 25–35 in R. Valencia & H. Balslev (editors), *Estudios sobre diversidad y ecología de plantas. Memorias del II Congreso Ecuatoriano de Botánica realizado en la Pontificia Universidad Católica del Ecuador*, Quito 16–20 Octubre 1995.
- . 1997c. *Xenophyllum*, a new Andean genus extracted from *Werneria* s.l. (Compositae: Senecioneae). *Novon* 7: 235–241.
- Gadek, P. A. J. J. Bruhl & C. J. Quinn. 1989. Exine structure in the 'Cotuleae' (Anthemideae, Asteraceae). *Grana* 28: 163–178.
- Hunziker, J. H., A. Wulff, C. C. Xifeda & A. Escobar. 1989. Estudios cariológicos en Compositae V. Darwiniana 29: 25–39.
- Jeffrey, C. 1979. Generic and sectional limits in *Senecio* (Compositae): II. Evaluation of some recent studies. *Kew Bull.* 34: 49–58.
- . 1986. The Senecioneae in east tropical Africa. *Notes on Compositae: IV*. *Kew Bull.* 41: 873–943.
- . 1992. The tribe Senecioneae (Compositae) in the

- Mascarene Islands with an annotated World check-list of the genera of the tribe. Notes on Compositae VI. Kew Bull. 47: 49–109.
- , P. Halliday, M. Wilmot-Dear & S. W. Jones. 1977. Generic and sectional limits in *Senecio* (Compositae): I. Progress report. Kew Bull. 32: 47–67.
- Kadereit, J. W. & C. Jeffrey. 1996. A preliminary analysis of cpDNA variation in the tribe Senecioneae (Compositae). In D. J. N. Hind & H. J. Beentje (editors), Compositae: Systematics. Proceedings of the International Compositae Conference, Kew, 1994. Vol. 1: 349–360. Royal Botanic Gardens, Kew.
- Keil, D. J. & T. F. Stuessy. 1975. Chromosome counts of Compositae from the United States, Mexico, and Guatemala. Rhodora 77: 171–195.
- King, R. M., D. W. Kyhos, A. M. Powell, P. H. Raven & H. Robinson. 1976. Chromosome numbers in Compositae, XIII: Eupatorieae. Ann. Missouri Bot. Gard. 63: 862–888.
- Knox, E. B. 1996. What is the origin of the giant senecios in eastern Africa? In D. J. N. Hind & H. J. Beentje (editors), Compositae: Systematics. Proceedings of the International Compositae Conference, Kew, 1994. Vol. 1: 691–703. Royal Botanic Gardens, Kew.
- & R. R. Kowal. 1993. Chromosome numbers of the East African giant Senecios and giant Lobelias and their evolutionary significance. Amer. J. Bot. 80: 847–853.
- & J. D. Palmer. 1995. The origin of *Dendrosenecio* within the Senecioneae (Asteraceae) based on chloroplast DNA evidence. Amer. J. Bot. 82: 1567–1573.
- Kowal, R. R. 1975. Systematics of *Senecio aureus* and allied species on the Gaspé Peninsula, Quebec. Mem. Torrey Bot. Club 23: 1–113.
- . 1994. Chromosome numbers of the aureoid senecios (*Packera*) and their evolutionary significance [Abstract.] P. 22 in D. J. N. Hind (coordinator), Compositae: Systematics Biology Utilization, Paper and Poster Abstracts.
- Lawrence, M. E. 1980. *Senecio* L. (Asteraceae) in Australia: Chromosome numbers and the occurrence of polyploidy. Austral. J. Bot. 28: 151–165.
- . 1985a. *Senecio* L. (Asteraceae) in Australia: Recombination systems of a polyploid series. Austral. J. Bot. 33: 209–219.
- . 1985b. *Senecio* L. (Asteraceae) in Australia: Nuclear DNA amounts. Austral. J. Bot. 33: 221–232.
- Liston, A. & J. W. Kadereit. 1995. Chloroplast DNA evidence for introgression and long distance dispersal in the desert annual *Senecio flavus* (Asteraceae). Pl. Syst. Evol. 197: 33–41.
- , L. H. Rieseberg & T. S. Elias. 1989. Genetic similarity is high between intercontinental disjunct species of *Senecio* (Asteraceae). Amer. J. Bot. 76: 383–388.
- Nordenstam, B. 1977. Senecioneae and Liabeae—Systematic review. Pp. 799–830 in V. H. Heywood, J. B. Harborne & B. L. Turner (editors), The Biology and Chemistry of the Compositae. 2 vols. Academic Press, London, New York, San Francisco.
- . 1978. Taxonomic studies in the tribe Senecioneae (Compositae). Opera Bot. 44: 1–83.
- . 1996a. *Jessea gunillae* B. Nord. (Compositae–Senecioneae), a new species from Costa Rica. Bot. Jahrb. Syst. 118: 147–152.
- . 1996b. Recent revision of Senecioneae and Calenduleae systematics. In D. J. N. Hind & H. J. Beentje (editors), Compositae: Systematics. Proceedings of the International Compositae Conference, Kew, 1994. Vol. 1: 591–596. Royal Botanic Gardens, Kew.
- . 1997. *Caucasalia*, a new genus of the Asteraceae, Senecioneae. Pl. Syst. Evol. 206: 19–32.
- & J. F. Pruski. 1995. Additions to *Dorobaea* and *Talamancalia* (Compositae–Senecioneae). Comp. Newsl. 27: 31–42.
- Ornduff, R., N. A. M. Saleh & B. A. Bohm. 1973. The flavonoids and affinities of *Blennosperma* and *Crocidium* (Compositae). Taxon 22: 407–412.
- , T. Mosquin, D. W. Kyhos & P. H. Raven. 1967. Chromosome numbers in Compositae, VI: Senecioneae II. Amer. J. Bot. 54: 205–213.
- , P. H. Raven, D. W. Kyhos & A. R. Kruckeberg. 1963. Chromosome numbers in Compositae, III: Senecioneae. Amer. J. Bot. 50: 131–139.
- Payne, W. W., P. H. Raven & D. W. Kyhos. 1964. Chromosome numbers in Compositae, IV: Ambrosieae. Amer. J. Bot. 51: 419–424.
- Pippen, R. W. 1968. Mexican “cacalioid” genera allied to *Senecio* (Compositae). Contr. U.S. Natl. Herb. 34(6): 363–447.
- Powell, A. M. & J. Cuatrecasas. 1970. Chromosome numbers in Compositae: Colombian and Venezuelan species. Ann. Missouri Bot. Gard. 57: 374–379.
- , D. W. Kyhos & P. H. Raven. 1974. Chromosome numbers in Compositae, X. Amer. J. Bot. 61: 909–913.
- , ——— & ———. 1975. Chromosome numbers in Compositae, XI: Helenieae. Amer. J. Bot. 62: 1100–1103.
- Radford, I. J., Q. Liu & P. W. Michael. 1995. Chromosome counts for the Australian weed known as *Senecio madagascariensis* (Asteraceae). Austral. Syst. Bot. 8: 1029–1033.
- Raven, P. H. & D. W. Kyhos. 1961. Chromosome numbers in Compositae, II: Helenieae. Amer. J. Bot. 48: 842–850.
- , O. T. Solbrig, D. W. Kyhos & R. Snow. 1960. Chromosome numbers in Compositae, I: Astereae. Amer. J. Bot. 47: 124–132.
- Robinson, H. 1981. A revision of the tribal and subtribal limits of the Heliantheae (Asteraceae). Smithsonian Contr. Bot. 51: i–iv, 1–102.
- . 1982. Pp. 309–313 in G. R. Proctor, More additions to the Flora of Jamaica. J. Arnold Arbor. 63.
- . 1983. A generic review of the tribe Liabeae (Asteraceae). Smithsonian Contr. Bot. 54: i–iv, 1–69.
- & R. D. Brettell. 1973a. Tribal revisions in the Asteraceae. IX. The relationship of *Ischnea*. Phytologia 26: 153–158.
- & ———. 1973b. Studies in the Senecioneae (Asteraceae). IV. The genera *Mesadenia*, *Syneilesis*, *Miricacalia*, *Koyamacalia* and *Sinacalia*. Phytologia 27: 265–276.
- & ———. 1974. Studies in the Senecioneae (Asteraceae). V. The genera *Psacaliopsis*, *Barkleyanthus*, *Telanthophora* and *Roldana*. Phytologia 27: 402–439.
- & J. Cuatrecasas. 1978. A review of the Central American species of *Pentacalia* (Asteraceae: Senecioneae). Phytologia 40: 37–50.
- & ———. 1992. Additions to *Aequatorium* and *Gynoxys* (Asteraceae: Senecioneae) in Bolivia, Ecuador, and Peru. Novon 2: 411–416.
- & ———. 1994. *Jessea* and *Talamancalia*, two new genera of the Senecioneae (Asteraceae) from Costa Rica and Panama. Novon 4: 48–52.
- & B. Kahn. 1986. Trinervate leaves, yellow flow-

- ers, tailed anthers, and pollen variation in *Distephanus* Cassini (Vernonieae: Asteraceae). *Proc. Biol. Soc. Wash.* 99: 493–501.
- , A. M. Powell, R. M. King & J. F. Weedin. 1981. Chromosome numbers in Compositae, XII: Heliantheae. *Smithsonian Contr. Bot.* 52: 1–28.
- , ———, ——— & ———. 1985. Chromosome numbers in Compositae, XV: Liabeae. *Ann. Missouri Bot. Gard.* 72: 469–479.
- , ———, G. D. Carr, R. M. King & J. F. Weedin. 1989. Chromosome numbers in Compositae, XVI: Eupatorieae II. *Ann. Missouri Bot. Gard.* 76: 1004–1011.
- Sindel, B. M. 1996. Impact, ecology and control of the weed *Senecio madagascariensis* in Australia. In P. D. S. Caligari & D. J. N. Hind (editors), *Compositae: Biology & Utilization. Proceedings of the International Compositae Conference, Kew, 1994*. Vol. 2: 339–349. Royal Botanic Gardens, Kew.
- Skvarla, J. J. & B. L. Turner. 1966. Pollen wall ultrastructure and its bearing on the systematic position of *Blennosperma* and *Crocidium* (Compositae). *Amer. J. Bot.* 53: 555–563.
- Solbrig, O. T., L. C. Anderson, D. W. Kyhos & P. H. Raven. 1969. Chromosome numbers in Compositae, VII: Astereae III. *Amer. J. Bot.* 56: 348–353.
- , D. W. Kyhos, A. M. Powell & P. H. Raven. 1972. Chromosome numbers in Compositae, VIII: Heliantheae. *Amer. J. Bot.* 59: 869–878.
- , L. C. Anderson, D. W. Kyhos, P. H. Raven & L. Rudenberg. 1964. Chromosome numbers in Compositae, V: Astereae III. *Amer. J. Bot.* 51: 513–519.
- Swenson, U. 1995a. Systematics of the Blennospermatinae (Asteraceae, Senecioneae). *Acta Univ. Ups., Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology* 162: 1–34. Uppsala.
- . 1995b. Systematics of *Abrotanella*, an Amphipacific genus of Asteraceae (Senecioneae). *Pl. Syst. Evol.* 197: 149–193.
- Tobgy, H. A. 1943. A cytological study of *Crepis fuliginosa*, *C. neglecta*, and their F1 hybrids and its bearing on the mechanism of its phylogenetic reduction in chromosome number. *J. Genet.* 45: 67–111.
- Tomb, A. S., K. L. Chambers, D. W. Kyhos, A. M. Powell & P. H. Raven. 1978. Chromosome numbers in Compositae, XIV: Lactuceae. *Amer. J. Bot.* 65: 717–721.
- Turner, B. L. 1970. Chromosome numbers in the Compositae. XII. Australian species. *Amer. J. Bot.* 57: 382–389.
- & W. H. Lewis. 1965. Chromosome numbers in the Compositae. IX. African species. *J. S. African Bot.* 31: 207–217.
- , J. H. Beaman & H. F. L. Rock. 1961. Chromosome numbers in the Compositae. V. *Rhodora* 63: 121–129.
- , A. M. Powell & J. Cuatrecasas. 1967. Chromosome numbers in Compositae. XI. Peruvian species. *Ann. Missouri Bot. Gard.* 54: 172–177.
- , ——— & R. M. King. 1962. Chromosome numbers in the Compositae. VI. Additional Mexican and Guatemalan species. *Rhodora* 64: 251–271.
- Villaseñor, J. L. 1986. Revisión de *Senecio* seccion *Mulgedifolii* (Compositae: Senecioneae). *Maestro en Ciencias (Biología) Tesis, Universidad Nacional Autónoma de México*.
- . 1991. The systematics of *Senecio* section *Mulgedifolii* (Asteraceae: Senecioneae). Ph.D. Thesis, Claremont Graduate School, Claremont, California.
- Vincent, P. L. D. 1996. Progress on clarifying the generic concept of *Senecio* based on an extensive world-wide sample of taxa. In D. J. N. Hind & H. J. Beentje (editors), *Compositae: Systematics. Proceedings of the International Compositae Conference, Kew, 1994*. Vol. 1: 597–611. Royal Botanic Gardens, Kew.
- Vision, T. J. & M. O. Dillon. 1996. Sinopsis de *Senecio* L. (Senecioneae, Asteraceae) para el Perú. *Arnaldea* 4: 23–46.
- Wagner, R. P., M. P. Maquire & R. L. Stallings. 1993. *Chromosomes: A Synthesis*. Wiley-Liss., New York.
- Webb, C. J. 1988. Notes on the *Senecio lautus* complex in New Zealand. *New Zealand J. Bot.* 26: 481–484.
- Wetter, M. A. 1983. Micromorphological characters and generic delimitations of some New World Senecioneae (Asteraceae). *Brittonia* 35: 1–22.

Appendix 1. General distributions, habit, and apparent basic chromosome numbers, geographical ranges, and habits of genera of the Senecioneae. Arrangement follows the genera and some of the groupings of Jeffrey (1992) with numerous modifications to coincide with discussions in the text.

Genus	General distribution	Habit	Chromosome number
Blennospermatinae			
<i>Blennosperma</i> Less.	W U.S., Chile,	annual herbs	$n = 7, 9$
<i>Crocidium</i> Hook.	W U.S.	annual herbs	$n = 9$
<i>Ischnea</i> F. Muell.	New Guinea	annual herbs	$n = 9$
Abrotanellinae			
<i>Abrotanella</i> (Gaudich.) Cass.	S South America, SW Pacific	perennial herbs	$n = 9, 18$
New Guinea Montane Endemic Group			
<i>Papuacalia</i> Veldkamp	New Guinea	woody	$n = 36$
Tussilagininae			
<i>Traversia</i> Hook. f.	New Zealand	shrubs	$n = 30$
<i>Bedfordia</i> DC.	Australia	small trees	$n = 30$
<i>Brachyglottis</i> J. R. Forst. & G. Forst.	New Zealand & Tasmania	shrubs	$n = 30$
<i>Telanthophora</i> H. Rob. & Brettell	Mexico, Central America	weak shrubs	$n = 30$
<i>Pittocaulon</i> H. Rob. & Brettell	Mexico, Central America	seasonally deciduous shrubs	$n = 30$
<i>Barkleyanthus</i> H. Rob. & Brettell	U.S., Mexico	shrubs	$n = 30$
<i>Roldana</i> La Llave	SW U.S., Mexico, Central America	subshrubs, shrubs	$n = 30$
<i>Digitacalia</i> Pippen	Mexico, Guatemala	perennial herbs	$n = 30$
<i>Psacalium</i> Cass.	U.S., Mexico	rosulate perennial herbs	$n = \text{ca. } 25, \text{ ca. } 29, 30$
<i>Pippenalia</i> McVaugh	Mexico	rosulate perennial herbs	$n = 30$
<i>Robinsonecio</i> T. M. Barkley & Janovec	Mexico, Guatemala	perennial herbs	$n = 30$
<i>Luina</i> Benth.	Mexico	subshrubs	$n = 30$
<i>Cacaliopsis</i> A. Gray	W U.S.	perennial herbs	$n = 30$
<i>Rugelia</i> Shuttlew. ex Chapm.	E U.S.	perennial herbs	$n = 28$
<i>Arnoglossum</i> Raf.	E U.S.	perennial herbs	$n = 25, 26, 27, 55$
<i>Tetradymia</i> DC.	W U.S., Mexico	shrubs	$n = 30$
<i>Lepidospartum</i> A. Gray	W U.S., Mexico	shrubs	$n = 30, \text{ ca. } 45$
<i>Dolichoglottis</i> B. Nord.	New Zealand	perennial herbs	$n = 30$
<i>Dendrocacalia</i> (Nakai) Nakai ex Tuyama	Bonin Island	weak shrubs	$n = 30$
<i>Farfugium</i> Lindl.	E Asia	perennial herbs	$n = 30$
<i>Ligularia</i> Cass.	Europe, Asia	perennial herbs	$n = 24, 27, 29, 30$
<i>Cremanthodium</i> Benth.	Asia	perennial herbs	$n = 29$
<i>Sinacalia</i> H. Rob. & Brettell	China	perennial herbs	$n = 30$
<i>Parasenecio</i> W. W. Sm. & Small	E Asia, Aleutians	perennial herbs	$n = 26, 29, 30, 60$
<i>Miricacalia</i> Kitam.	Japan	perennial herbs	$n = 26, 27$
<i>Syneilesis</i> Maxim.	E Asia	perennial herbs	$n = 26, 39$
<i>Doronicum</i> L.	Europe	perennial herbs	$n = 15, 20, 30, 60$
<i>Homogyne</i> Cass.	Eurasia	perennial herbs	$n = 30, 60, 70, 80$
<i>Tussilago</i> L.	Eurasia	perennial herbs	$n = 30$
<i>Endocellion</i> Turcz.	N & E Asia	perennial herbs	$n = 28, 29, 30$
<i>Petasites</i> Mill.	Eurasia, North America	perennial herbs	$n = 14, 16, 26, 28, 30$
<i>Sinosenecio</i> B. Nord.	S & SE Asia, W North America	perennial herbs	$n = 23, 24$
<i>Nemosenecio</i> (Kitam.) B. Nord.	E Asia	perennial herbs	$n = 24$
<i>Tephroseris</i> (Rchb.) Rchb.	Central Europe, Arctic	perennial herbs	$n = 24, 25$